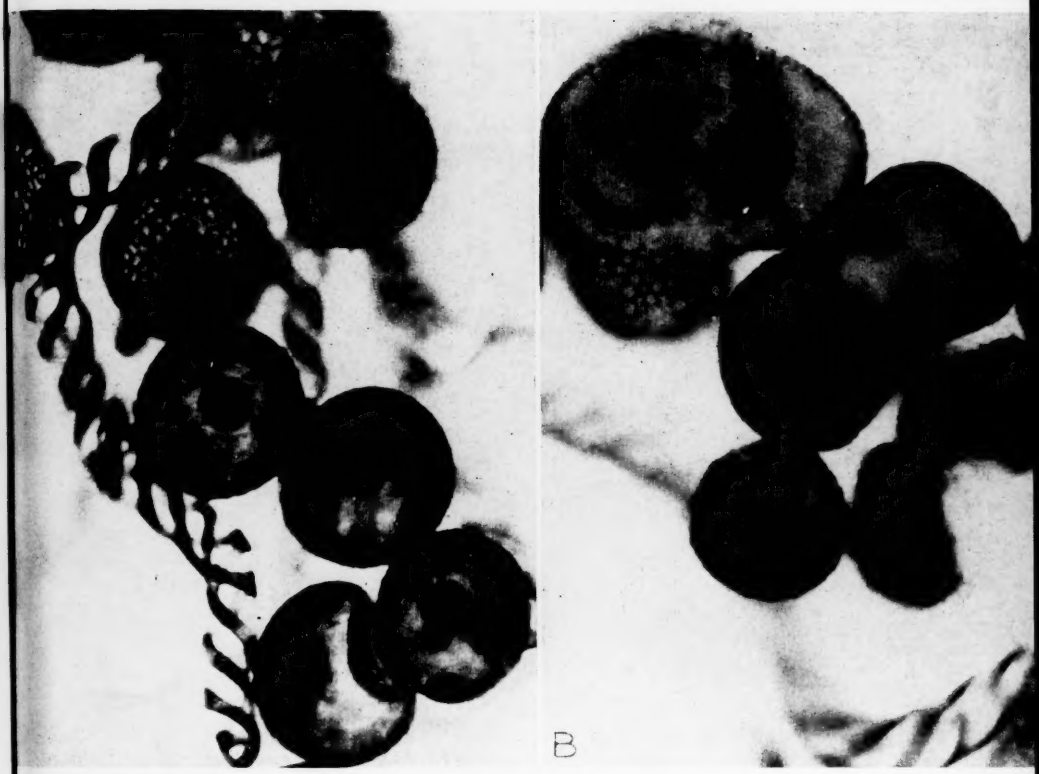
The Journal of HEREDITY



EFFECT OF COLCHICINE ON LIVERWORT SPORES

(See page 67)

A Bluegrass Hybrid

Sex-Linked Albinism of the Fowl

A Map of Drosophila's Third Chromosome

Absorption Spectrum of the Body Wall

VOLUME 32 FEBRUARY, 1941 NUMBER 2

The American Genetic Association

An incorporated organization devoted to promoting a knowledge of the laws of heredity and their application to the improvement of plants, animals, and human racial stocks

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Debtors to Science

★

All civilization, to be sure, is indebted to the men of science.

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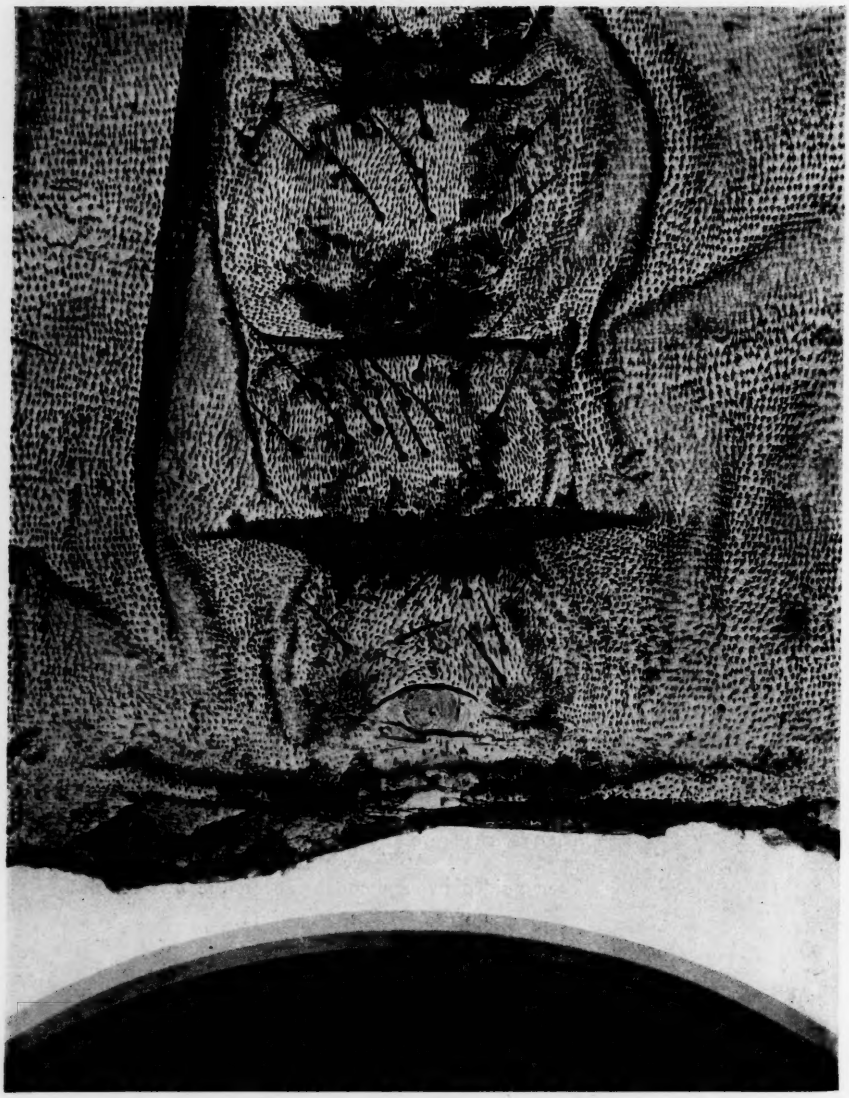

PORTRAIT OF SPECIMEN NO. 5 (v-w) AT 2750 A

Frontispiece

Abdominal wall of a specimen of *Drosophila melanogaster* prepared for ultraviolet transmission study. The bristles appearing in the center of the photograph are on the midline of the belly. The folds in the skin are due to flattening out a normally curved surface. This photograph is made with monochromatic light of 2750 Angstrom units wavelength. (×115.)

ULTRAVIOLET ABSORPTION SPECTRUM OF THE ABDOMINAL WALL OF DROSOPHILA MELANOGASTER

ERIC DURAND,* ALEXANDER HOLLAENDER,† AND M. B. HOULAHAN‡

THE effect of ultraviolet radiation on the production of lethal mutations in *Drosophila melanogaster* has been described in a number of publications. Altenburg[1] and Geigy[2] used the entire radiation of quartz mercury vapor lamps; Mackenzie and Muller[3] used broad regions of the mercury spectrum isolated by filters, and Demerec and Hollaender[4] investigated the effects of certain monochromatic wavelengths on the appearance of lethal mutations. In most of these investigations the sperm was irradiated while still present in the living male fly. For a quantitative interpretation of the efficiency of different wavelengths in producing such mutations, it is necessary to know how much of the radiation is absorbed by the different tissues in the path from the abdominal wall to the sperm in the testis. As a first step in this study the absorption spectrum of the abdominal wall between 2140 and 4400A of two strains of *Drosophila* was determined.

Experimental Procedure

Male flies of the strains *Swedish-b* and *yellow-white* were used. The flies were etherized, and the thorax and tip of the abdomen, including about half of the sixth segment, were cut off. The remaining portion of the abdominal wall was split longitudinally along the dorsal side, flattened out, and scraped as nearly free as possible of muscle and viscera. The wall was then washed in a solution of glycerin in water and mounted in glycerin, with the internal surface of the wall next to the quartz cover slip.

The photomicrography was done with the Zeiss quartz ultraviolet microscope (Köhler[5]), using the 16 mm, N. A. 0.20 objective, the N. A. 0.20 condenser, and the 5× and 10× oculars. Magnifications between 100 and 200 were used. Separate quantitative observations were made with each monochromatic wavelength, as had been done previously by Caspersson,[6] and others. The actual technique employed here was that developed by Cole and Brackett,[7] using a rotating step-sector disk directly in front of a photographic plate. The disk had 11 steps, with an intensity range of 70 to 1. Eastman types 33, II-0, and II-0 ultraviolet sensitized photographic plates were used. A schematic diagram of the apparatus is given in Figure 3. Densities were measured with a Bausch and Lomb Photronic Cell Densitometer.

The light sources used were a cadmium spark, and high-pressure capillary mercury arcs, Westinghouse types AH-3 and AH-4, with the outer pyrex jacket removed.

The first specimens were photographed in sharp focus at each wavelength. Such a series is shown in Figure 1. However, it was found to be unnecessarily difficult to make densitometric measurements of all of the detail showing; hence subsequent specimens were photographed with the objective depressed 100μ below the position of sharp focus§ (which was determined for each wavelength). Figure 2.

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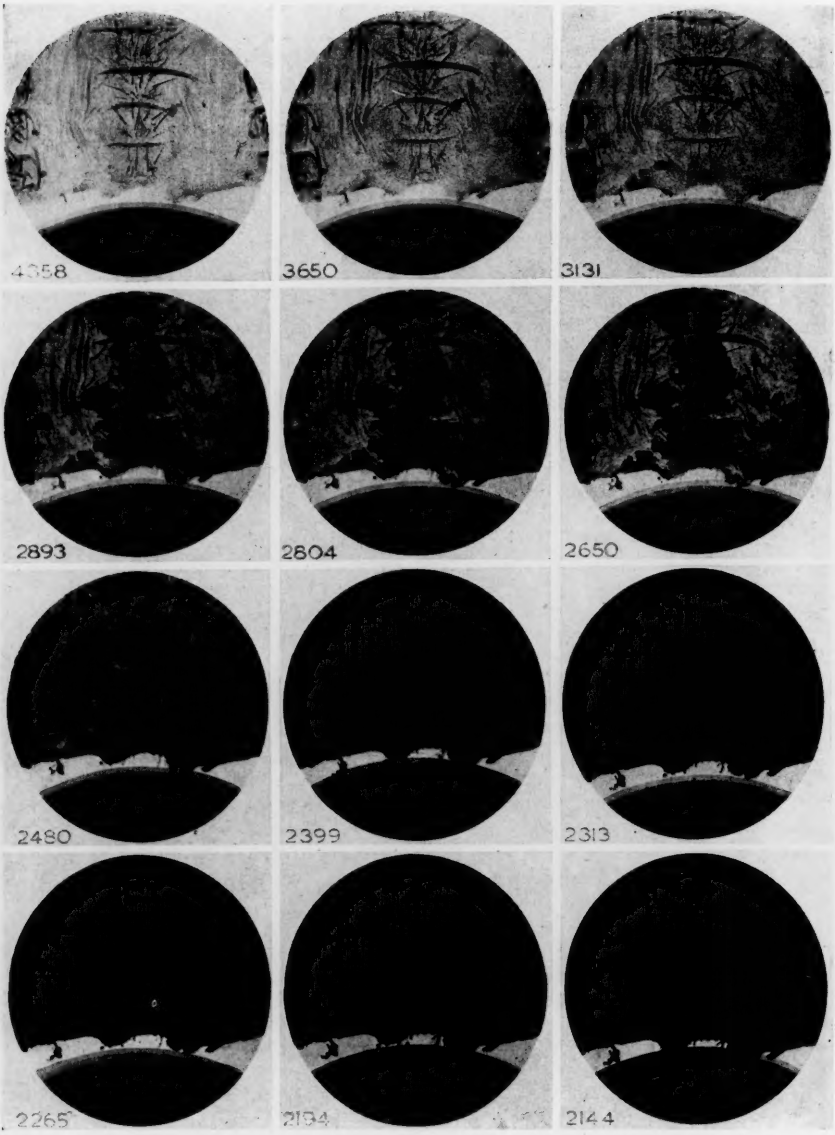
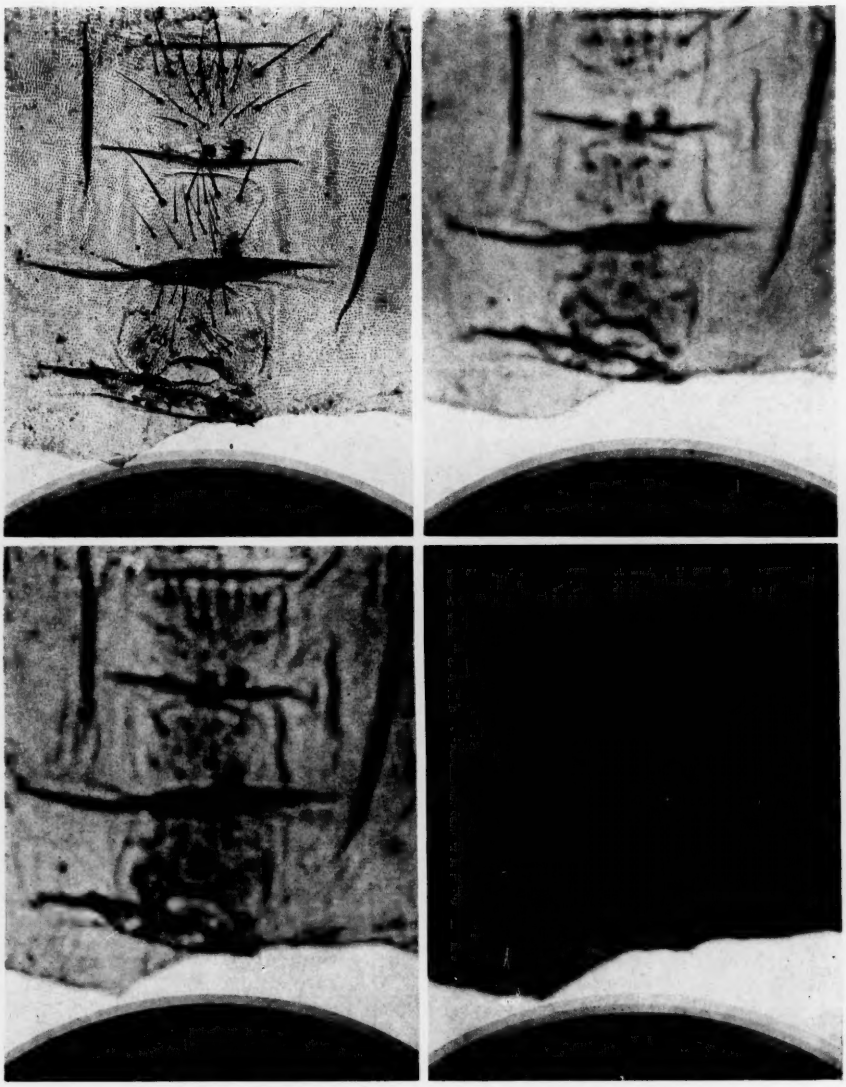
§If the area measured by the densitometer covers regions of varying density (i.e. detail), the resulting deflection is *not* a measure of the average transmission. If the detail is obliterated by defocusing the microscope, a more correct value will be obtained.



SHORT WAVELENGTHS ABSORBED BY ABDOMINAL WALL

Figure 1

In-focus body-wall of a single specimen (No. 2 *Sw.-b.*) photographed at progressively shorter wavelengths of ultraviolet light beginning at 4358A. Note the density scale produced on the bottom of each photograph by the shadow of the rotating step-sector disk (Figure 3). The density range was necessarily shortened in preparing the photographs for reproduction, e. g. in the negative taken at 2144A, all eleven steps of the scale showed clearly, although only four may be seen in the reproduction. Magnification ×35.



TYPICAL OUT-OF-FOCUS PLATES

Figure 2

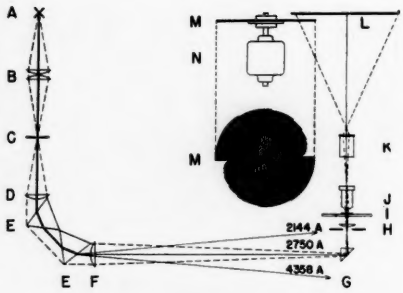
Three typical out-of-focus plates (*B-D*) of specimen No. 4 (*y-w*) at different wave-lengths. All plates used in the measurements were thrown the same amount out of focus, so that the blurring of details would be uniform. An in-focus plate at 2750A is shown for comparison (*A*). Magnification ×57.

For reference purposes a sharply focused photograph of each specimen was taken at 2750A. One such photograph is reproduced in the Frontispiece.

In all, seven specimens were prepared, of which two were studied in focus. Twenty-three wavelengths were used, but only 16 appear in the final runs, this number being considered sufficient to establish the shape of the curves. Five areas on each of two flies were measured for each strain. No significant differences in absorption between the two strains appeared, so the data for both strains were averaged and plotted in a single curve. In every case, only the clearest areas were measured, i.e., dark areas due to folds, bristles, or patches of abdominal tissue were avoided. (See also below.)

From the photographs, such as Frontispiece, one might judge the bristles to be completely opaque. Visual observation with white light shows them to be translucent, if not transparent, with a brownish color. It is not possible, however, to estimate the absorption coefficient relative to the clear wall, since the thickness of the latter is not known, and since refractive effects add a spurious absorption to the bristles.

Several regions of abnormal opacity appeared on the earlier preparations (Figure 1). These are regions where bits of abdominal tissue cling to the wall, and are absent in the later, more carefully cleaned, specimens (Figure 2 and Frontispiece).



SCHEMATIC DIAGRAM OF THE APPARATUS

Figure 3

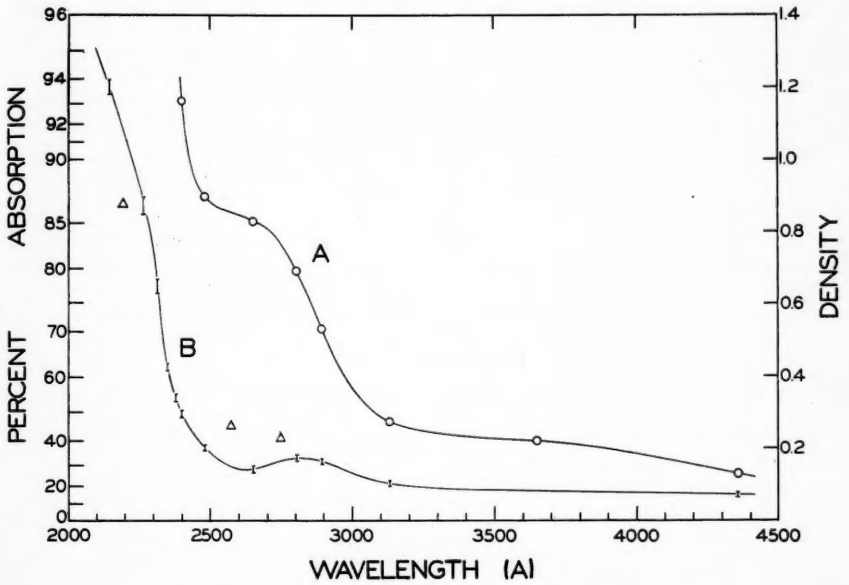
The intensity scale on the photographs (Figures 1 and 2) is the "shadow" of the rapidly rotating step-sector disk (*M*). *A*—Light Source; *B*—Condensers; *C*—Circular Monochromator entrance "slit"; *D*—Collimating Lens; *E*—Cornu Prisms; *F*—Camera Lens; *G*—90° Reflection prism; *H*—Substage Condenser and Diaphragm (Monochromator selector "slit"); *I*—Quartz slide and cover-slip; *J*—Objective; *K*—Ocular; *L*—Photographic Plate; *M*—Step-sector disk (actual photograph); *N*—D. C. Motor.

Results

Curves of the results are given in Figure 4. Curve *A* represents the average absorption of several points along the dark central patch of the specimen shown in Figure 1. For wavelengths shorter than 2399A, the absorption of this area was beyond the limits of the method.

Curve *B* shows the average transmission at each wavelength of the twenty selected points on the four specimens of the main run. The vertical lines at some of the experimental points are the "probable errors" as calculated statistically from the variations among the twenty individual values which go to make up each point. These cannot be taken as the actual probable errors of the results, since several sources of systematic error, such as scattering and time effect (see below) may be present. They are, however, a measure of the degree to which one may reduce errors due to the true variability of the biological material.

The data from which Curve *B* was drawn indicated absorption structure at 2750, 2573, and 2194A. This structure was suspected of being spuriously introduced by the fact that each of these wavelengths had been photographed a day or more after the others (due to the exigencies of changing from arc to spark, etc.), or by some possible difference in measurement with arc and spark lines. The latter cause was ruled out by making comparative photographs of a new specimen at the same wavelength with both types of sources (e.g. 2752 Hg, and 2748 Cd). Photographs of the same



ABSORPTION CURVES OF ABDOMINAL WALL

Figure 4

A—Central portion of Specimen No. 2. Large absorption is due to a layer of adherent tissue of unknown thickness. *B*—Average for Specimens No. 2-6. Taken within five hours after preparation of the specimens. Lengths of vertical lines show statistical probable errors. Triangles are isolated points taken from 24 to 48 hours after preparation. See text.

specimen taken under identical conditions several days apart showed substantial changes in absorption. Therefore, only the points obtained from the fresh preparations have been included in the curve. Points obtained from old preparations are shown as isolated triangles (△).

Discussion

Perhaps the most unexpected result of this study is the finding of the high transparency of the abdominal wall to most wavelengths. Chitin is the main constituent of the wall, and the qualitative work of Eloff and Bosazza[8] on the absorption of the chitin in the wings of the locust *Nomdacris septemfasciator* had indicated a much higher absorption than was found here.

Chitin, according to Karrer,[9] "has the characteristics of a complex polysaccharide." It is similar to cellulose but is more resistant to attack by micro-organisms. The low absorption in the region 2400 to 4400A is characteristic of many polysaccharides, as is the small maximum at 2800 A, which is probably due to a ring structure. Furthermore, Miller[10] suggests a wall thickness of only 2-5μ, so that one would find a low absorption even for moderately large values of the absorption coefficient.

Curves of the individual areas show considerable variability, which is larger than the probable error of measurement,

and furthermore, is systematic, i.e., some areas are more opaque at *all* wavelengths; others more transparent. In addition, significant systematic variations appear between the averages for the individual flies. These variations are probably due to differences in the thickness of the layer measured, rather than to differences in the absorption coefficients.

The rapid increase in the absorption of the patches, which sets in below 3000 A, indicates that large absorption of energy must take place in the tissues between the wall and the testes. Therefore, in order to determine the energy absorbed by the sperm, and hence actually available for the production of mutation, one must determine the absorptive properties of intervening layers of abdominal tissue including the sperm wall. The character of these intervening layers is well known through the work of Miller[10] who has studied the position of the testes in the abdominal cavity under a variety of conditions. It is planned to extend the study of absorptive properties with the ultraviolet microscope to these other intervening layers.

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✦

Animal Longevity

STORIES about animals with average life-spans of 100, 150, or even 200 years are usually flights of someone's imagination, declare officials of the Fish and Wildlife Service, United States Department of the Interior. "As a matter of fact," one scientist said, "man probably has a higher life expectancy rate than any other animal known, with the possible exception of the tortoise."

Available information is inadequate for establishing definite averages, the scientists pointed out, because little work has been done on the life span of animals, but conservative observers make estimates far below the popular idea.

In some instances, it is suspected, long-lived animals like the elephants are credited with being much older than they actually are because of errors in records handed down from one owner to another. It is thought that animals probably live longer in captivity than in the wild.

The elephant's life span has been set at 100 or more years, but records show that it is between 40 and 50 on the average. The oldest record for an elephant in captivity is 78 years, as reported in the *Journal of the Bombay Natural History Society* in 1933.

Most tortoises, it is believed, go to their happy hunting grounds between their 50th and 60th birthdays, although cases of extreme old age have been reported.

Among other animals whose average life span is debunked are the following: Falcons, credited with living as long as 162 years, are believed to live only 7 to 10. A vulture 118 years old is far older than most of its brothers and sisters, who according to some observers, die between the ages of 15 and 20. Golden eagles are more likely to live to 18 or 20, not 100; swans 15, instead of 100; and geese 16 to 20, instead of 200 years. The parrot's reputed life span of 200 years dwindles to about 17, while a 40-year-old crocodile can be said to have lived 4 times longer than the average member of the clan.—*Wildlife Clipsheet—U. S. Dept. of the Interior.*

AN ARTIFICIAL HYBRID BETWEEN TWO SPECIES OF BLUEGRASS

Canada Bluegrass (*Poa compressa* L.) and Kentucky Bluegrass (*P. pratensis* L.)

WM. H. BRITTINGHAM
*U. S. Regional Pasture Research Laboratory**
State College, Pennsylvania

TWO artificial hybridizations between species of *Poa* have been previously reported. The earliest recorded hybridization is that by Oliver[4] in 1908 who crossed a female plant of the dioecious species, *Poa arachnifera* (Texas Bluegrass) with *P. pratensis* (Kentucky Bluegrass). He obtained a highly variable F_1 progeny. More recently E. Marion Brown[4] has repeated this cross. His F_1 progeny also was quite variable and included plants more resistant to heat and drought and more productive than Kentucky Bluegrass. The second species cross in *Poa* was first reported by Åkerberg[1] who pollinated a semi-sterile plant of *P. pratensis* with pollen of *P. alpina* (Alpine Bluegrass) and obtained a progeny of 17 plants, one of which was a hybrid. Chromosome counts indicated the fertilization of a reduced ovule of *pratensis* by a reduced pollen grain of *alpina*. The other plants of the progeny resembled the *pratensis* mother, implying apomictic development stimulated by *alpina* pollen (pseudogamy). Müntzing[2] also reports a *Poa pratensis* × *alpina* cross.

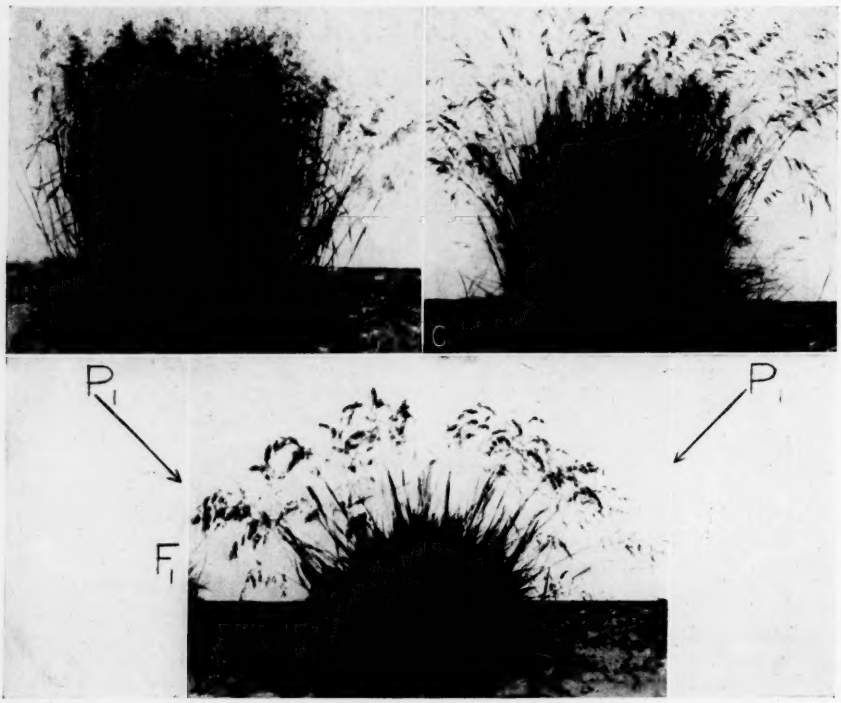
This paper describes an artificially produced hybrid between *Poa compressa* (Canada Bluegrass) and *P. pratensis* (Kentucky Bluegrass). The author is not aware of any previous report of a hybrid between these species.

Origin of the Hybrid

The hybridization between Canada Bluegrass and Kentucky Bluegrass was accomplished in the greenhouse at the U. S. Regional Pasture Research Laboratory during the winter of 1938. The Canada Bluegrass plant was obtained from a commercial seed lot and may be considered representative of *Poa compressa* (Figure 5*A*). The Kentucky Bluegrass plant was obtained in a progeny from seed of a single panicle collected in a West Virginia pasture. It is approximately the "average plant type" for *P. pratensis* (Figure 5*C*). No difficulty was experienced in inducing the two parents to flower at the same time in the greenhouse, although under field conditions at State College the Kentucky Bluegrass parent precedes the Canada Bluegrass parent by ten days to two weeks.

Emasculation was attempted using the hot water technique first proposed by Stephens and Quinby.[3] It was found in Canada Bluegrass that a temperature of 45° C. was the highest which allowed subsequent near-normal anthesis and seed set. The time of treatment varied between five and ten minutes. Inconclusive results were obtained in this attempt to adapt the hot water emasculation technique to *Poa*. The results may be due either to the fact that reproduction by apomixis in the Canada Bluegrass parent is unusually pronounced as determined by the character of its progeny, or to the failure of the hot water to destroy the pollen at a sub-lethal temperature for the ovules. The writer is inclined to the former explanation particularly in view of the fact that his results parallel so closely those of Åkerberg just cited and also because Stephens and Quinby had success with tempera-

*Contribution No. 20 from the U. S. Regional Pasture Research Laboratory, Division of Forage Crops and Disease, Bureau of Plant Industry, U. S. Department of Agriculture, in cooperation with the Department of Agronomy, University of Maryland, and the Northeastern States.



PARENT AND HYBRID PLANTS

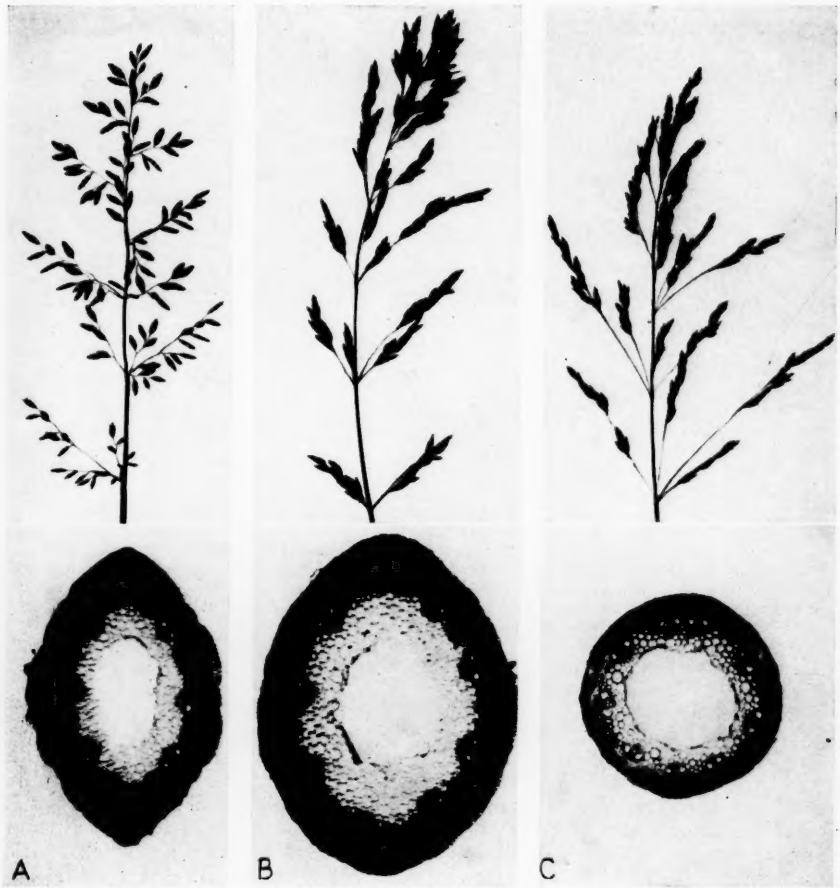
Figure 5

Growth habits of the mature plants photographed at their respective flowering dates. *A*—Canada Bluegrass female parent, photographed June 20. *B*—Canada × Kentucky Hybrid, photographed June 14. *C*—Kentucky Bluegrass male parent, photographed June 8.

tures lower than 45° C. Whatever the cause, all but one of the 42 plants from the attempted cross were unmistakably like the Canada Bluegrass mother plant. However, this individual in a progeny of three plants from a 45° C. five-minute treatment was very clearly different, having somewhat thicker and more glossy leaves. Differences became more and more pronounced as further growth ensued. For example, this atypical plant was the only one of the 42 seedlings from the attempted cross which failed to flower in the greenhouse during the spring of 1939. The plants were placed in the field that fall and the parents, the hybrid, and its sibs flowered in June, 1940.

Description of the Hybrid

The appearance of the Canada-Kentucky hybrid in the field at flowering time is shown in Figure 5*B*. Comparable photographs of the Canada Bluegrass and Kentucky Bluegrass parents are given in Figure 5*A* and *C*, respectively. A very evident character possessed by the hybrid plant is its comparative lack of stemminess. Both of the parent plants are decidedly stemmy, the Canada parent to an extreme degree. In the hybrid, however, length of the leaf sheaths is

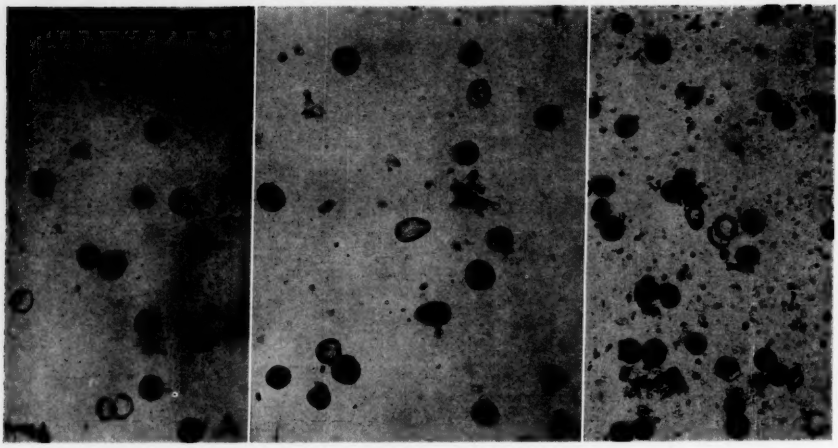


PANICLES AND STEM SECTIONS

Figure 6

Representative panicles of parents and hybrid at times of flowering, two-thirds natural size. *A*—Canada Bluegrass female parent. *B*—Canada × Kentucky Hybrid. *C*—Kentucky Bluegrass male parent. Below the panicles are shown cross-sections of the culms of parents and hybrid. These were cut from the base of the panicle and were photographed without staining, ×37. The dominance of the shape of the Canada culm is clearly shown, as well as considerable hybrid vigor.

materially reduced, so that the leaves grow very much closer to the ground. Leaves of the hybrid are intermediate in length and width between the characteristically short, wide leaves of Canada Bluegrass and the rather long, narrow leaves of the Kentucky Bluegrass parent. The leaves of the Canada Bluegrass



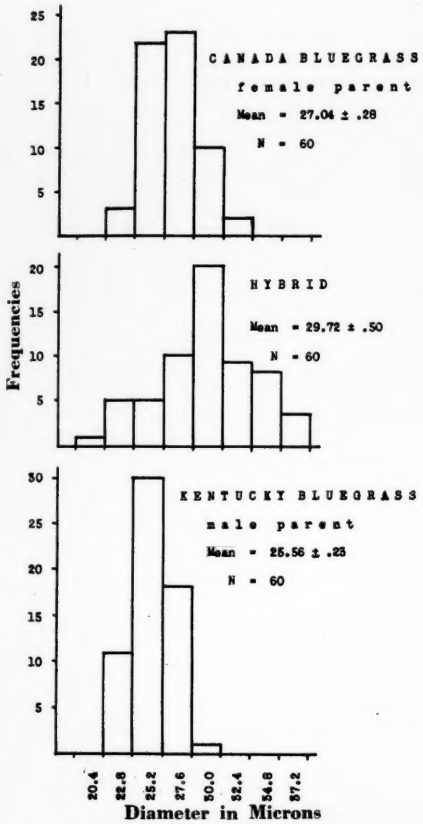
HYBRID POLLEN GRAINS LARGER

Figure 7

Photomicrographs of pollen grains at time of flowering. *A*—Canada Bluegrass; *B*—Canada × Kentucky hybrid; *C*—Kentucky Bluegrass. All three forms produce considerable bad pollen. The measureably larger grain of the hybrid was the first clue to its chromosome constitution. It has two complete sets of Canada Bluegrass chromosomes and one set of Kentucky chromosomes. Acetocarmine preparations. ×130.

parent are a dull, bluish green; those of the Kentucky Bluegrass parent are a bright, light green, while leaves of the hybrid are a bright, very deep green. The hybrid plant possesses good vigor, and first year observations indicate good spreading qualities. While it is somewhat intermediate between the two parents in *degree* of spread, the hybrid plant in *type* of spread resembles the Kentucky parent with its well developed extensive rhizomes. In this description of vegetative characters, the observation of the first year regarding disease response and the persistence of green color of the foliage after flowering should be mentioned. The hybrid was particularly outstanding. It maintained its leafiness and good green color well into August, whereas both the parent plants, particularly Canada Bluegrass, went into summer dormancy a few weeks after flowering. It was noticed also that leaves of the hybrid were relatively free from leaf spot and rust, while these diseases were severe on the parents. Observations in the greenhouse indicated that all three plants are susceptible to mildew, but it seemed less extensive and severe on the hybrid.

Comparative flowering habits of the Canada-Kentucky Bluegrass hybrid and its parent species are illustrated in Figure 5. It is seen that the hybrid is not as prolific in panicle formation as either of the parents. The Canada parent is a very prolific seeder; the Kentucky parent is also a heavy seeder but represents the "average" rather than the most prolific of the species. Considering the future practical use to which hybrids in forage grasses will probably be put, it is gratifying to see this moderate though adequate production of seed heads in the hybrid. Panicles of the hybrid are longer, larger and much heavier than those of either parent. Representative panicles of the three plants are shown in Figure 6*A-C*. The contrast between the hybrid



POLLEN-GRAIN DIMENSIONS

Figure 8

Measurements of mature pollen grains of the Canada Bluegrass female parent, the Kentucky Bluegrass male parent, and their hybrid.

and its Canada Bluegrass parent is very striking. The spikelets of the hybrid are considerably larger and more numerous per panicle. An interesting difference among the panicles of the three forms was found in a study of cross sections of the culm at the base of the panicle. The results are an additional indication that hybridization between the two species, *Poa compressa* and *Poa pratensis,* has been accomplished. Photomicrographs of unstained, free-hand sections are also shown in Figure 6*A-C*. The specific character of the compressed culm of Canada Bluegrass is shown in Figure 6*A;* the evenly rounded culm of Kentucky in Figure 6*C;* and the intermediate shape and increased area of the culm of their hybrid in Figure 6*B*. Considering the ratio of width to length as an index, we find in Kentucky Bluegrass a ratio of 1:1; in Canada Bluegrass a ratio of 1:1.47; while in the Canada-Kentucky hybrid an intermediate ratio of 1:1.29. Just as in the macroscopic features of the hybrid panicle there appears to be hybrid vigor, so here, also, it may be seen. Reducing actual measurements to relative areas and designating the area of Kentucky Bluegrass as 1.00, we find that Canada Bluegrass has a relative area of 1.28 and the hybrid a relative area of 1.96.

Seed Set and Germination in the Hybrid

The date of flowering was determined as that time at which three or more panicles were well in bloom. Only one season's observations are available. In the spring of 1940 at State College, the Kentucky Bluegrass parent flowered on June 8, followed by the Canada-Kentucky hybrid on June 14, and this in turn followed by the Canada Bluegrass parent on June 20. Flowers of the hybrid bloomed well, the anthers dehisced properly and there was ample pollen. The hybrid and its parents were bagged, with parchment bags in triplicate. The Canada parent set seed very poorly under bag, not over 20 per cent. In one bag of the three no seed was obtained. In the Kentucky parent, on the other hand, seed set under bag was about 80 per cent. The hybrid plant also produced seed very well under bag. not as abundantly as the Kentucky parent, but more than the Canada parent. Its seed set under bag was about 60 per cent. Seed was also obtained from the hybrid under open pollination, and the yield was very good. Seed from the hybrid is appreciably larger and heavier than seed from either of its parents. Some idea of this difference in seed size may be had by comparing the average weights of representative lots of 100 open

pollinated seed from the three plants. The average weights for 100 seeds of the Canada Bluegrass parent and the Kentucky Bluegrass were .022 gm. and .024 gm. respectively. The average weight for 100 seeds of the hybrid was .034 gm, an increase in weight of 45.4% over Canada and of 41.7% over Kentucky.

Open pollinated seed of the hybrid and of the Canada and Kentucky parents collected in July, 1940, was germinated at room temperature in Petri dishes in October, the seed being approximately three months old. Several hundred seed of each plant were tested. Germination of seed of Canada Bluegrass was 83.2% (927 out of 1,114), of Kentucky Bluegrass 78.6% (707 out of 900), and of the hybrid 68.5% (638 out of 930). Twin seedlings appeared in 2.58% of the Canada Bluegrass seedlings (24 in 927), in 8.34% of the Kentucky Bluegrass seedlings (59 in 707), and in 5.95% of the seedlings of the hybrid (38 in 638). There is a highly significant difference between the frequencies of twinning in Canada and Kentucky ($\chi^2 = 27.32$) a highly significant difference between Canada and the hybrid ($\chi^2 = 11.78$), and an insignificant difference between Kentucky and the hybrid ($\chi^2 = 2.85$).

Pollen Size and Chromosome Number

As has been shown repeatedly in numerous polyploid species and genera, there is a positive correlation between cell size and chromosome number. This has recently been shown to be true for *Poa pratensis* by Müntzing.[2] Accordingly an attempt was made to estimate the chromosomal number in the Canada-Kentucky hybrid by the measurement of pollen grains. Pollen was collected at anthesis, and acetocarmine slides prepared. Only full grains were measured. The mean diameters in microns are as follows: Canada Bluegrass parent 27.04 ± .28, Kentucky Bluegrass 25.56 ± .23, and the hybrid 29.72 ± .50 (Figure 7*A*, *B*, *C* and Figure 8). There is a highly significant difference between the measurements of pollen grains in the Canada Bluegrass mother plant and in the hybrid between this plant and Kentucky Bluegrass. The difference is 2.68 ± .58 microns and t = 4.62.

The pollen of both Canada and Kentucky Bluegrass was comparatively uniform in size and shape. Empty grains were few in Canada but reached a frequency of about 10% in Kentucky. The pollen of the hybrid, on the other hand, was very variable in size and contained over 60% shriveled and empty grains. A consistent feature of the pollen of the hybrid was the high proportion of irregular and pear-shaped grains. Assuming the pollen of *Poa* to be a sphere for purposes of comparison, the volumes in cubic microns, determined from the mean diameters, are as follows: Canada Bluegrass parent 10,331, Kentucky Bluegrass 8,716, and the hybrid 13,689. The volume of the pollen grain of the hybrid represents a 32.4% increase over the volume of the pollen grain of Canada Bluegrass. From this information, it was decided that the hybrid plant very likely had a higher chromosome number than either parent. Considering further

TABLE I. A compilation of quantitative data from parents and hybrid.

	Canada Bluegrass parent	*Canada-Kentucky hybrid*	*Kentucky Bluegrass parent*
Date of flowering	6/20/40	6/14/40	6/8/40
Ratio of width to length of culm in cross-section	1:1.47	1:1.29	1:1
Relative area of culm in cross-section	1.28	1.96	1.00
Mean diameters in microns of pollen grains	27.04±.28	29.72±.50	25.56±.23
Av. weight in grams of 100 seeds	0.022	0.034	0.024
Germination of three mon. old open pollinated seed	83.2%	68.5%	78.6%
Frequency of twin seedlings	2.58%	5.95%	8.34%
2n chromosome number	42	±72	56

the fact that the progeny tests conducted with the Canada Bluegrass parent have shown absolute uniformity of population, indicating a high degree of apomixis, it was thought that the hybrid plant may have arisen through the fertilization of an unreduced Canada chromosome complement by Kentucky pollen.

Chromosome counts of the hybrid and of the parent plants have been obtained from root-tip cells. The Canada Bluegrass female parent has a somatic number of 42 chromosomes, the Kentucky Bluegrass male parent a somatic number of 56, and the Canada-Kentucky hybrid a somatic number of ± 72. The method of origin of the hybrid is very clearly indicated. The chromosome numbers are consistent with the assumption that it represents the union between a cell of the Canada female parent having an unreduced number of 42 chromosomes and a pollen grain of the Kentucky parent carrying the approximately reduced number of 28-31 chromosomes. Accordingly, the hybrid has had a "triploid" origin, to use the term loosely. The Canada parent is hexaploid and the Kentucky parent octaploid. The hybrid thus becomes a decaploid, with six genoms of *Poa compressa* and four genoms plus of *P. pratensis*.

Summary

A hybrid plant was obtained between Canada Bluegrass, as female parent, and Kentucky Bluegrass, as pollen parent. The hybrid is not as stemmy as either parent, its leaves are dark green and are intermediate in length and width. First year observations indicate good vigor and good spreading qualities. The hybrid produces fewer panicles but they are larger and heavier. Seed is produced well both under bag and under conditions of open pollination. In several quantitative characters the hybrid is intermediate and in others it exceeds both parents, as is shown in Table I. The data indicate that the hybrid between these species has resulted from the union of an unreduced cell of *compressa* and an approximately reduced pollen grain of *pratensis*.

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✦

Today's Idols

AT THE head of my list is the study of what I shall call social images. The first great philosopher of science spoke of the invisible idols men erect and worship. Three of his four orders of idols were socially created, the idols of the tribe, the idols of the marketplace, and the idols of the theater. These images have frequently been exorcized by the logician and the philosopher, and more recently they have been described by the historian and in some part by the psychologist. A few sociologists, like Pareto, Veblen, and Thurman Arnold, have dealt with them in some fashion. But little enough has been done by way of the direct investigation of them. It is the business of the other sciences to eschew these idols; it is the business of the social sciences to study them. They are among the most portentous phenomena of social life. They are so powerful that at this hour, in most lands, men do not dare to look them in the face, so powerful that they make all science bow before them and furnish the technological aids they require for their greater power and glory. In all countries, they are enthroned and command allegiance. For these social images are more than idols—they are the projection of our social values, of our group and national solidarities, of the things that bind us and divide us also, group from group, nation from nation.—Robert M. McIver, in *Sociological Review,* Vol. 6, p. 4.

A REVISED MAP OF THE LEFT LIMB OF THE THIRD CHROMOSOME OF DROSOPHILA MELANOGASTER

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THE present map is the third in the series of revisions which is being carried out for the salivary gland chromosomes of *Drosophila melanogaster,* the two previous ones being of the *X*-chromosome[2] (published in this JOURNAL in 1938), and of the 2*R*-chromosome[3] (published in 1939). Those two, and the present 3*L*-chromosome map, serve as supplements to the map of 1935, the main features and divisions being retained substantially as they were.

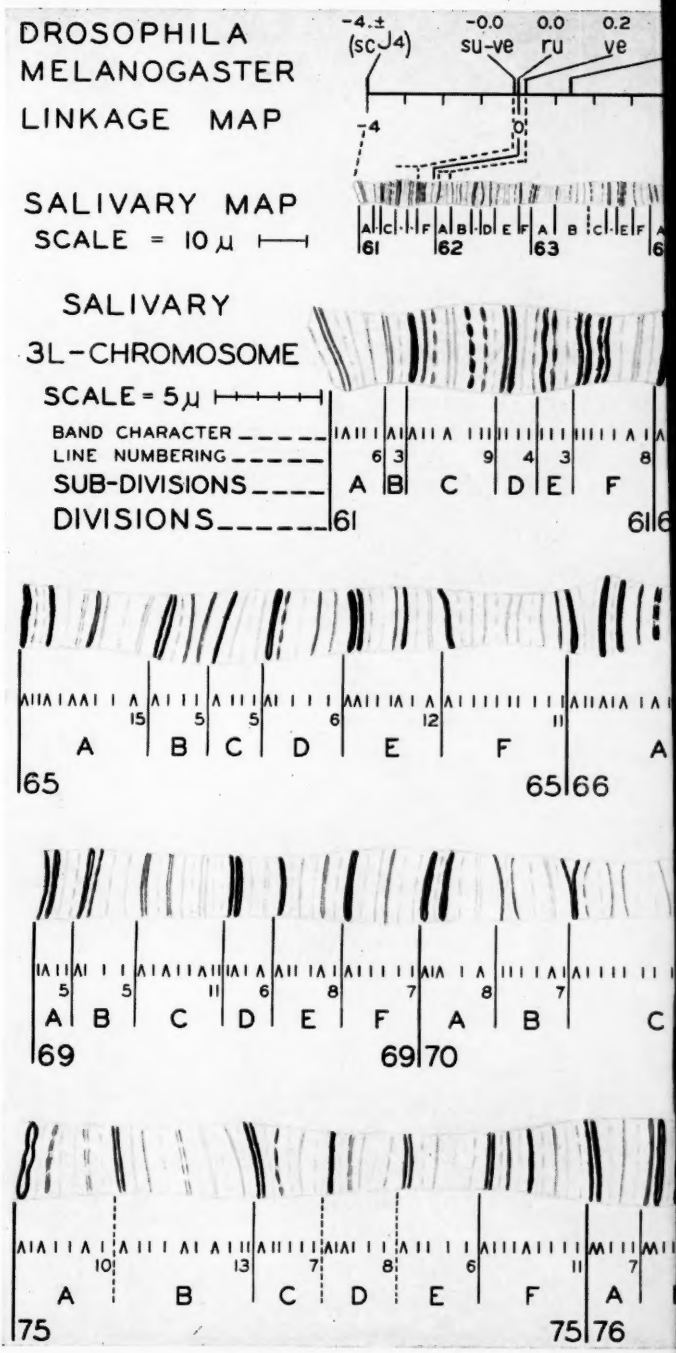
Permanent aceto-carmine smears of larval salivary glands, prepared as described in *DIS*-6, which involves using specially cultured larvae, dissection and fixation under chilling conditions, dehydration by the vapor replacement method, and mounting in euparol or Diaphane, was the material used for this revision, as in the former ones. Slides prepared according to this method are very transparent and clear, and the chromosomes are sharply defined and well stained, with little or no capsulation of the heavy bands.

Chromosomes for the revision were selected for favorable conditions of staining and stretching, freedom from kinks and mechanical distortion, and an average of seven camera lucida drawings for each section was made from these selected preparations at a magnification of 5,000 diameters. The revision consists of a generalized average of this series of drawings, its dimensions being averages of the lengths and widths of the separate drawings. The individual bands were then filled in by comparison of all the drawings, disagreements in number and character being checked by reference both to the original preparations and to new ones selected for this checking, the closest compatible structure to all these being taken as the standard for the map.

Many faint bands in addition to those indicated in the 1935 map have been found, and the characterization of all bands has been improved, many lines originally pictured as single now being analyzed as doublets or capsules, and former capsules are now often designated as close double bands. The relative intensities of the bands are better represented. This map is of value in that the revised banding is adequate for special studies without the need of making a new revision for each new problem. The map, however, represents a chromosome of medium stretch, hence allowance must be made for different amounts of stretch and difference in proportionate distances when more lax or more extended chromosomes are used.

The previous limits of the major divisions, as marked on the 1935 map, have been retained in all but one case, that of section 79. Seventeen sub-division lines have been moved to make use of somewhat heavier bands, or to equalize the sub-divisions as much as possible, and three sub-divisions have been added in section 80. Wherever a change from the 1935 map has been made it has been indicated by dashing the division marker.

The new map shows 884 bands as compared to the 542 on the 1935 map. The length of the present revision is 424 micra as compared to the 210 micra of the old. Choice of larger chromosomes and use of sections of greater and more uniform stretch account for the difference in these dimensions. The 3*L* revision is a generalized composite with a length intermediate between the lax chromosomes and the maximally stretched



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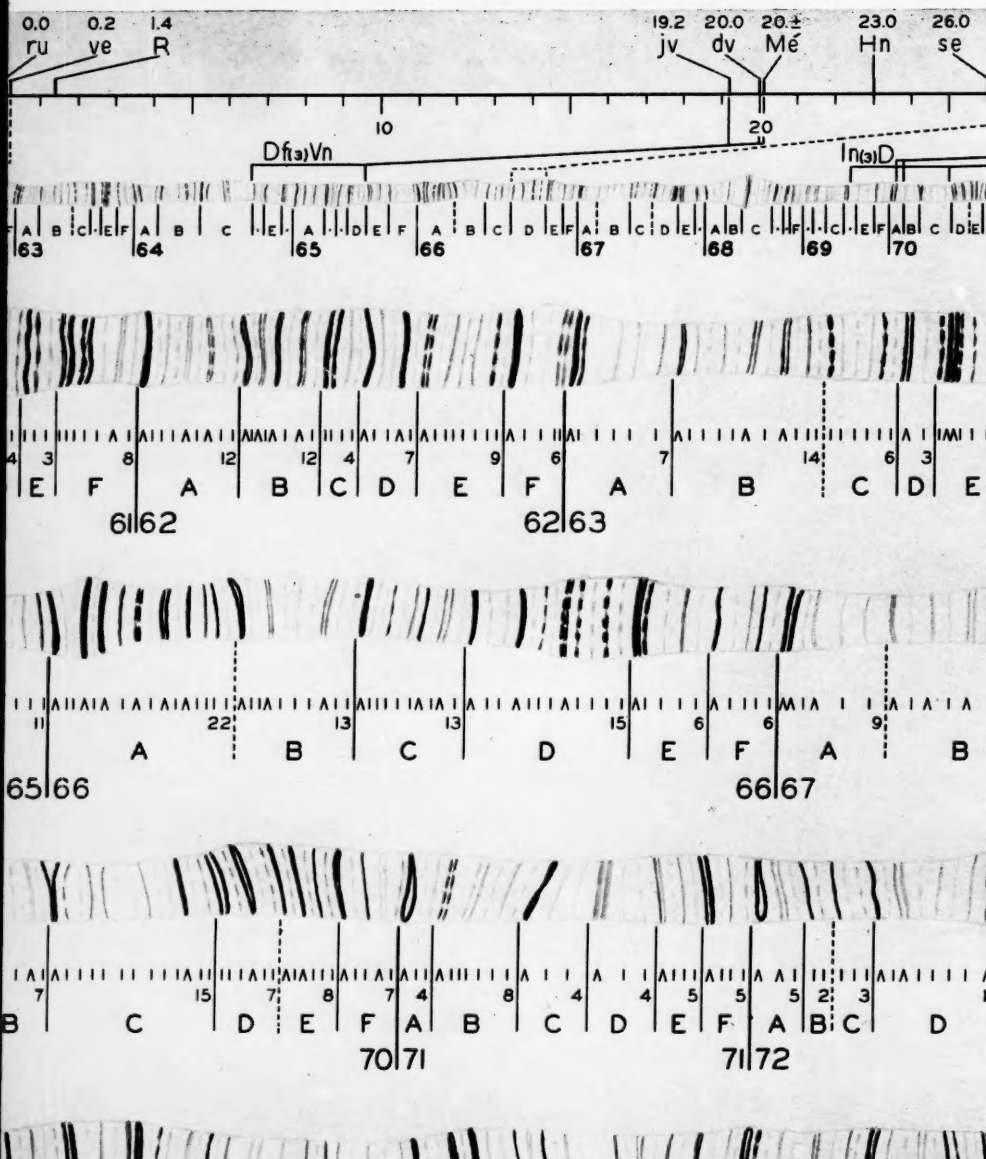

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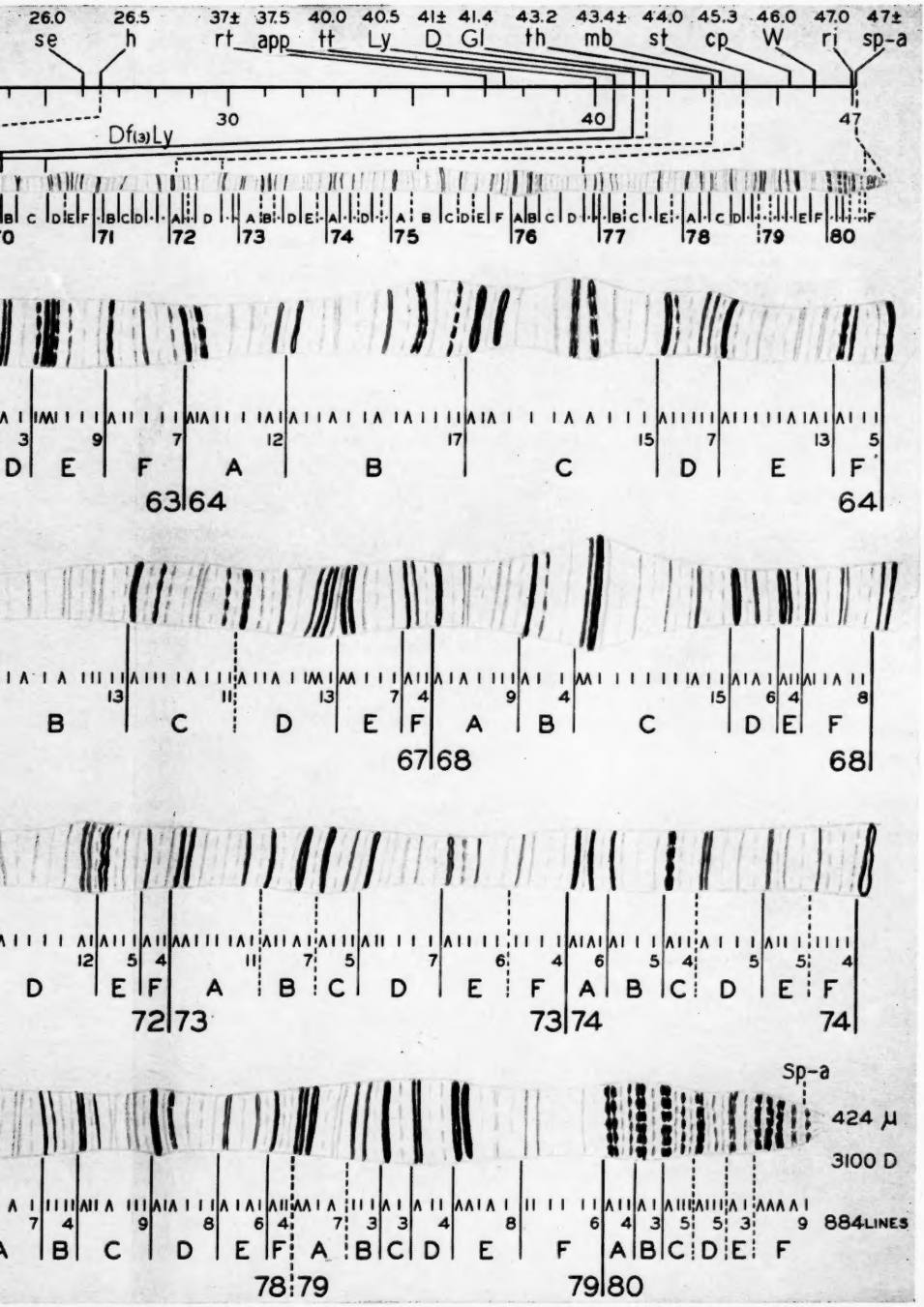

RENCE MAP OF THE SALIVARY GLAND 3L CHROMOSOME OF *DROSOPHILA MELANOGASTER.*

Figure 9

ones usually found in preparations. As such it shows many bands which will not show on shorter chromosomes, and shows many doubles which will appear single in the lax ones, while chromosomes stretched more than the map may show two lines where one was represented, and may even resolve a few extra faint ones.

Regions particularly difficult to analyze were the chromocentric region (division 80), where the banding is diffuse and irregular, tending to become granular; several regions where the banding is diffuse and foggy, other regions where the lines are faintly staining and spread apart, and certain sections where the banding becomes confused and irregular in many preparations. This latter usually happens where there are several heavy bands close together, and which seems to disorganize the chromosome into a knot, often causing the strand to break at such a point.

The diffuse, foggy regions most noted are in *64C*, with wide, nebulous bands, *68C*, where the chromosome puffs out, *71C-71E*, *72D*, *74D*, and *79E, F*,—of which the one in 71 is the most marked, the chromosome often breaking in this section. Faintly staining regions include *63A, B, 67A, B* (which is very noticeable); the beginning of section 70; most of section 74, *75A, B; 76C, D;* and the very noticeable *79E, F* region. Parts where heavy bands knot the chromosome are most marked in *64B*, where four heavy doublets are often irregular, *67D*, with a series of four or five dark bands, and *75C*, which is a point particularly susceptible to breaking.

For comparison of the linkage and chromosome maps the upper line of the figure gives the latest revision of the position of genes of the left half of the third chromosome as arranged in *DIS*-9. The lower line gives the present salivary revision at two-ninths' (approximately one-fourth) the linear magnification of the detailed map below. The two lines are connected wherever possible to show the salivary position of the genes. Solid lines indicate positions located with reasonable accuracy, while dotted lines indicate positions located only approximately within certain limits.

Most of the salivary correspondences were located according to data given in the symbol list of *DIS*-9, and in the symbol list revisions of *DIS*-12, making use of the information given on inversion, translocation, and deficiency limits and inclusions. The extension of the linkage map to —4 is made possible by Muller's work on sc^{J4}, the gene *ru* is located from unpublished data, as is *h*. The spindle-fiber attachment is located certainly to the right of *80E1.2*, according to the salivary configuration of an unpublished translocation of Demerec, and is probably as far right as *80F9*, according to studies of the salivaries by the author.

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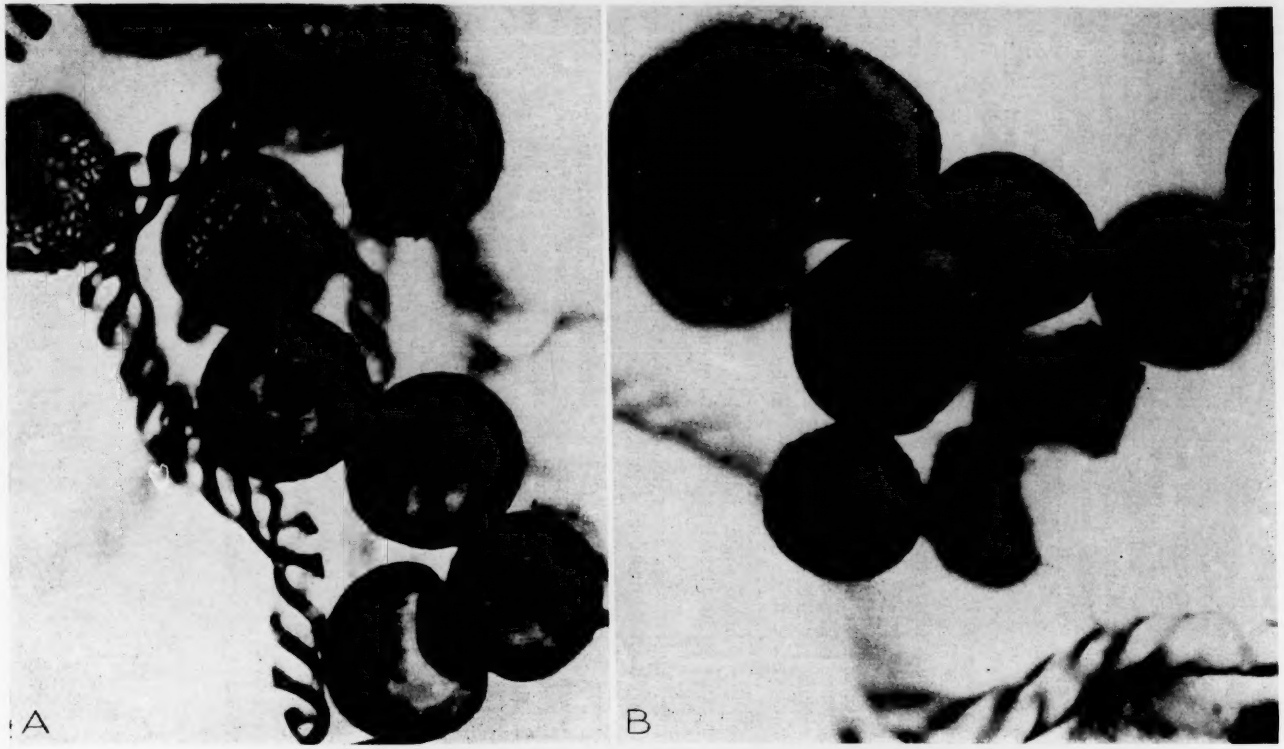

NORMAL AND COLCHICINE-TREATED SPORES

Figure 10

Photomicrographs of aceto-carmine smears. *A*—Normal spores and elaters. *B*—Tetrad, dyad, and monad spores from colchicine treated capsule. Colchicine treatment has greatly altered the normal spore formation processes, and this is not limited to cell division. (×1250.)

THE EFFECT OF COLCHICINE ON A HEPATIC

GORDON B. WOLCOTT
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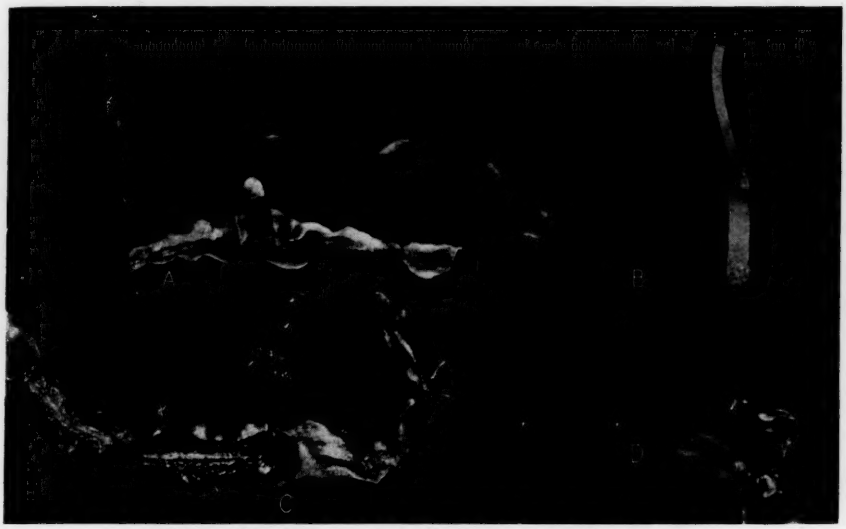


MALE AND FEMALE LIVERWORT GAMETOPHYTES

Figure 11

A—Female gametophyte of *Pallavicinia lyellii* with sporophyte enclosed within the perianth. *B*—Mature sporophyte exserted beyond the perianth. *C*—Male gametophyte with antheridia in two rows, one on either side of the midrib. *D*—Sterile gametophyte. Approximately ×3.

CERTAIN of the thallose liverworts, because of their relatively simple structure, should be favorable material for a morphogenetic study of intra-specific anenploidy.

Races of *Pallavicinia lyellii* (Hook.) Gray have been found by the author[1] with chromosome numbers of $n = 8$, $2n = 16$ and of $n = 9$, $2n = 18$. In order to obtain *Pallavicinia* with other aneuploid chromosome numbers a $2n = 18$ race, collected near Milano, Texas, was subjected to the action of colchicine. Although this phase of the work has not been completed, certain effects of colchicine on *Pallavicinia* are here reported.

In *Pallavicinia lyellii*, as in all Bryophytes, the gametophytic portion of the life cycle is greatly prolonged in contrast with the condition in higher plants. *Pallavicinia* is dioecious, an antheridia-bearing male gametophyte being distinct from a female plant on which archegonia are formed. The fertilized egg cell in an archegonium develops into a simple sporophyte which retains its connection with the gametophytic plant. The spore-mother-cells in the capsule of a sporophyte undergo meiosis during late winter. The spores are released by a splitting of the capsule wall and are disseminated by the twisting of elater cells formed in the capsule. Following germination the spores develop into gametophytes.

Treatment of Gametophytes

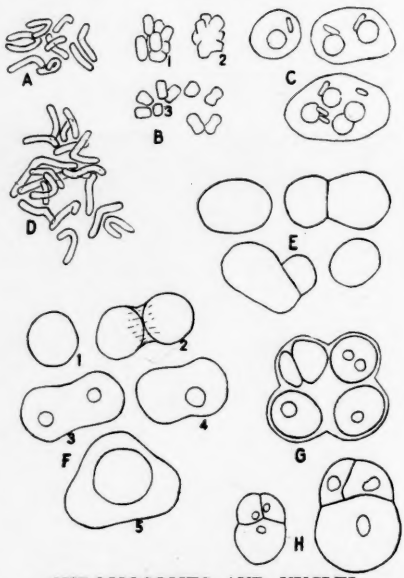
Whole gametophytes (3-4 cm. in length) were immersed in 1.0%, 0.5%, 0.25%, and 0.12% solutions of colchicine (Malinckrodt) and left for periods varying from five to 48 hours. Some growing tips were fixed immediately after removal from colchicine. The remainder were placed in a moist chamber. At one day

intervals for several days growing tips were removed from the chamber and fixed. Examination of the nuclear condition was by aceto-carmine smears following fixation in Carnoy's fluid, and by the section method.

The marked clumping of the chromosomes seen in Figure 12 *B*1 and *B*2 was found in all metaphase nuclei examined immediately after removal from colchicine. Associated with the clumping was a longitudinal contraction of the chromosomes shown best in Figure 12*B*3 in which the chromosomes are spread out by pressure of the cover slip. Clumping and contraction persisted for as much as three days after removal from colchicine. O'Mara[4] has described a similar longitudinal contraction of the chromosomes of *Allium Cepa* but observed the converse of clumping in that colchicine caused a spreading of the chromosomes throughout the cell. After three days haploid and diploid metaphase plates with normal distribution of the chromosomes were found. Figure 12*D* shows a doubled nucleus during metaphase in which the longest and shortest chromosomes, with their counterparts, may be located.

In *Pallavicinia* there is a single heteropycnotic chromosome in each haploid nucleus, and two such chromosomes in each diploid nucleus. Likewise there is a single nucleolus-forming chromosome, and therefore a single nucleolus, in each haploid nucleus, and two nucleolus-forming chromosomes, with their nucleoli, in each diploid nucleus. In diploid nuclei the two nucleoli may fuse[6]. Figure 12*C* is an outline drawing of a resting haploid nucleus from an untreated gametophyte, and of resting diploid and tetraploid nuclei from a gametophyte after colchicine treatment. The nuclei in Figure 12*C* show all heteropycnotic chromosomes and all nucleoli. There is an expected fusion of nucleoli within some of the nuclei from treated plants. The number of heteropycnotic chromosomes or of nucleoli (where fusion does not occur) affords a means of determining approximately the chromosome complement of the resting nuclei.

Sections of colchicine treated thalli showed haploid, diploid, and tetraploid nuclei. As yet no extensive sector of polyploid cells has been found. Satina (vide Blakeslee[1]) has produced diploid male and female gametophytes of *Marchantia polymorpha* by colchicine treatment of gemmae. This method cannot be applied to *Pallavicinia* since this species does not produce gemmae. The production of a polyploid apical cell by the use of colchicine would presumably produce



CHROMOSOMES AND NUCLEI

Figure 12

A—Haploid chromosome complement from the male thallus of *Pallavicinia*. *B*—Metaphase nuclei from sexually undifferentiated thallus fixed immediately after colchicine treatment. *C*—Normal haploid resting nucleus from untreated thallus, and resting nuclei from colchicine treated thalli showing increased number of nucleoli and of heteropycnotic chromosomes. *D*—Diploid chromosome complement from colchicine treated male thallus. (*A-D*, ×875.) *E*—Abnormal spores from colchicine treated capsule. *F*—Tetrad, dyad, and monad spores from treated capsule showing differences in the effect of colchicine on spore formation. (*E-F*, ×375.) *G*—Aberrant spore formation in an untreated capsule. (×280.) *H*—Sporelings of three cells grown from spores from treated and untreated capsules. (×195.) *E*—From living material, all others from aceto-carmine smears.

by growth an entire thallus homogeneous as to chromosome number. One hundred fifty plants, of both sexes, were treated with 0.5% colchicine for five hours and are now being grown in a moist chamber in an attempt to obtain homogeneously polyploid thalli.

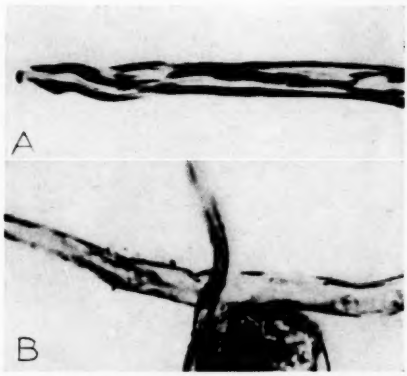
Sporogenesis and Elater Formation

The spore mother cells of *Pallavicinia* are differentiated and become four-lobed during the winter months. Meiosis does not occur until spring. Spore capsules turn dark immediately following meiosis due to the formation of a heavy reticulum over the surface of the spores, and the deposition of thickenings on the walls of the capsule cells. Gametophytes bearing sporophytes on which the capsules were full grown, but still green, were selected and the perianth carefully removed from around the capsule. These gametophytes were then immersed in colchicine in the same manner as the gametophytes without capsules. Results were obtained as follows:

1. 1.0% colchicine for nine hours. One capsule contained normal tetrad spores. Spores from other capsules were mixed tetrad spores, dyad spores, and monad spores (four-lobed, as in Figure 12 *F5*).
2. 0.5% colchicine for ten hours. One capsule contained normal tetrad spores; another contained mixed normal, dyad, and monad spores. (Figure 10*B*). The remaining capsules contained monad spores, with less than one per cent normal spores estimated.
3. 0.12% colchicine for 11 days. The plants were left in the colchicine until the dark color of the capsule indicated maturation of the spores. The spores from these capsules were highly irregular (Figure 12*E*) with many shrunken spores.
4. 0.12% colchicine for 23 days. Plants were left in the colchicine until the capsules turned dark. The spores were mostly irregular but one capsule contained all monad spores.

The normal elongation of the seta following spore maturation did not take place in any of the treated sporophytes.

Although dyad spores do occur in nature in *Pallavicinia*, especially in certain races, they were extremely rare in the clone used for this study. In untreated capsules there was an estimated three per cent aberrant spores. This included all shrunken, undersized, or enlarged spores. Normal spores and elaters from an untreated capsule are shown in Figure 10*A*. The capsules containing normal spores following colchicine treatment may be accounted for by assuming that the meiotic divisions had taken place just prior to the immersion in colchicine, but that the capsule had not yet turned dark.



COLCHICINE RELAXES ELATERS
Figure 13

Photomicrographs of unstained elaters from colchicine treated capsules. The structure of normal elaters is shown in Figure 10*A*. (700×.)

In the capsule containing normal spores, dyads, and monads (from experiment 2, above) there was a gradation in the effect of the colchicine on the spores as shown in Figure 12*F* in which *1* is one member of a normal tetrad, *2* shows a complete cellular cleavage with the spores still attached, and *3* a spore in which cell cleavage has been inhibited, but spindle formation has not, thereby producing a binucleate dyad. Figure 12 *F4* is a dyad with, presumably, a diploid nucleus, though this condition could not be critically ascertained in spore nuclei. A complete suppression of nuclear division and of cleavage of the spore mother cell is shown in Figures 10*B*, and 12*F5*.

Moore[3] states that in the spore mother cell of *Pallavicinia lyellii* the spore tetrads are delimited by cell plates on the meiotic spindle uniting with the furrows of the spore mother cell wall. His figures of this are not conclusive in that they show only the cell plate on the spindle, and fail to show any lateral growth of the cell plate or its union with the furrows. In a clone of *Pallavicinia* from

Charlottesville, Virginia, the author has found aberrant formation of spore cells, an example of which is shown in Figure 12*G*. There has been a cell division in an anucleate cell, which precludes spindle formation and cell plate formation. The binucleate dyad shown in Figure 12 *F3* shows nuclear division without cell division. These observations indicate that, as in the formation of microspores in some higher plants (Sharp[5], page 167), cytokinesis in spore mother cells of *Pallavicinia* is independent of spindle formation. The effect of colchicine as a suppressor of cell cleavage in the spore mother cell may be considered as an effect separate from the suppression of spindle formation.

The two spiral thickenings on the elaters of *Pallavicinia* (Figure 10*A*) are formed on the walls of the elaters during the time that the spores are maturing.[2] There was an abnormal formation and distribution of the thickenings in colchicine treated capsules (shown in Figure 13*A*). No abnormal elaters were found in capsules with normal spores, whether exposed to colchicine or not. With one exception (from which Figure 10*B* was taken) in all capsules in which colchicine had affected sporogenesis the elaters were abnormal. Figure 13*A* illustrates an elater in which the thickenings were well formed but spiralling was inhibited; Figure 13*B* shows an almost complete lack of thickening in the wall. There was a gradation in the suppression of the formation of spiral thickenings from nearly normal to the condition shown in Figure 13*B*. The suppression of the formation of spiral thickenings on the walls of the elaters indicates an intra-cellular action of colchicine on cells which are not undergoing division.

Germination

Spores from all capsules containing monad spores were sown on moist filter paper. Spores from untreated capsules were used as a control. The initial step in the germination of *Pallavicinia* spores is a swelling which in the monad spores obliterated the lobes. Figure 12*H* shows a sporeling of the monad spore and a sporeling of the same stage from a normal tetrad spore. A large number of haploid and polyploid sporelings were transplanted to Benecke's nutrient solution in an attempt to grow them.

Conclusions

From the foregoing observations it is evident that the action of colchicine in the cells of *Pallavicinia* is similar to that in higher plants. There is the usual inhibition of spindle formation, but not of chromosome division, resulting in nuclei with a doubled number of chromosomes. The action of colchicine on spore mother cells undergoing meiosis produces spores with, presumably, diploid or tetraploid nuclei, depending on the number of meiotic spindles suppressed.

The action of colchicine on the cells of *Pallavicinia* is not confined to the spindle mechanism. The effect on the chromosomes is a strong longitudinal contraction (Figure 12*B*). Associated with the contraction is a marked clumping of the chromosomes shown in Figure 12 *B1-2* which may indicate an effect on the chromosomes or on the cytoplasm surrounding them. An effect on the cytoplasm in cells in which the nucleus is not in a state of mitotic activity is shown by the suppression of the formation of spiral thickenings on the walls of developing elater cells, or a departure from the pattern in which this material is usually distributed (Figure 13). The suppression of cleavage, or furrowing, in the spore mother cell by colchicine (Figures 12*F* and 10*B*) is an effect on the cytoplasm of the cell independent of the effect on the spindle mechanism.

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GENETICS OF THE FOWL

12—Sex-Linked, Imperfect Albinism

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IN the spring of 1939, a pink-eyed chick, dingy white in color, was found among pure Barred Plymouth Rock chicks hatched at a nearby chick hatchery. Knowing our interest in such "sports," Mr. Monroe Babcock, owner of the hatchery, very kindly brought the chick to us for further study. As it grew older, there became evident in the new feathers (which were white) faint bars (Figure 14) which gave the plumage the appearance of being what Punnett[9] has aptly described as "ghost-barred." This attested to the Barred Plymouth Rock parentage.

The chick turned out to be a female. Genetic analysis was facilitated because the bird, which came from a strain of Barred Rocks bred for high egg-production, matured early and laid well. About a year after receipt of the original chick, it was clear that the deficiency of melanin was caused by a sex-linked, recessive gene.

Description

A. Plumage

At hatching, the albinotic chicks vary in appearance from practically pure white to a dusky chocolate color. In those carrying barring, the chicks are usually dark enough to show by contrast the unpigmented occipital head spot produced in the down by the gene for barring (Figure 16). As such chicks grow, the barring pattern becomes faintly visible in the juvenile and adult plumage. The ghost bars of the barred albino apparently correspond to the black bars in feathers of a normal Barred Plymouth Rock, but seem much narrower (Figure 17).

Matings of F_1 males, heterozygous for barring, silver, and albinism, with New Hampshire (red) females showed that the gene inhibits red and gold as effectively as it does black pigments. In such a mating, one would expect half the progeny to show the sex-linked gold color, if albinism were not involved. Whereas many of the fully-pigmented chicks, both males and females, did show gold, no sign of red or gold was visible in the albinos. Carotinoid pigments in the shanks and skin are not affected by the albinism.

For microscopic examination, barbs of down and of definitive feathers were dehydrated in ethyl alcohol, cleared in toluene, and mounted, unstained, in Diaphane. Barbs from albinos genotypically black or barred appeared under low magnification to be creamy brown in color. At higher magnification, these barbs were found to contain a number of scattered rod-shaped granules of melanin, but nothing like the dense mass of pigment found in black feathers (Figure 18).

B. Eye

White plumage is in itself no proof of albinism‡ especially in the fowl where the White Leghorn, White Wyandotte, and many other white varieties have fully pigmented eyes. Since with increasing degrees of albinism the eye is the last place to lose its melanin, careful examination of that structure was necessary to determine what grade of albinism is caused by the mutation. At hatching time the albinotic chicks have bright pink eyes. This appearance is caused by the blood in the eye, which in normal fowls

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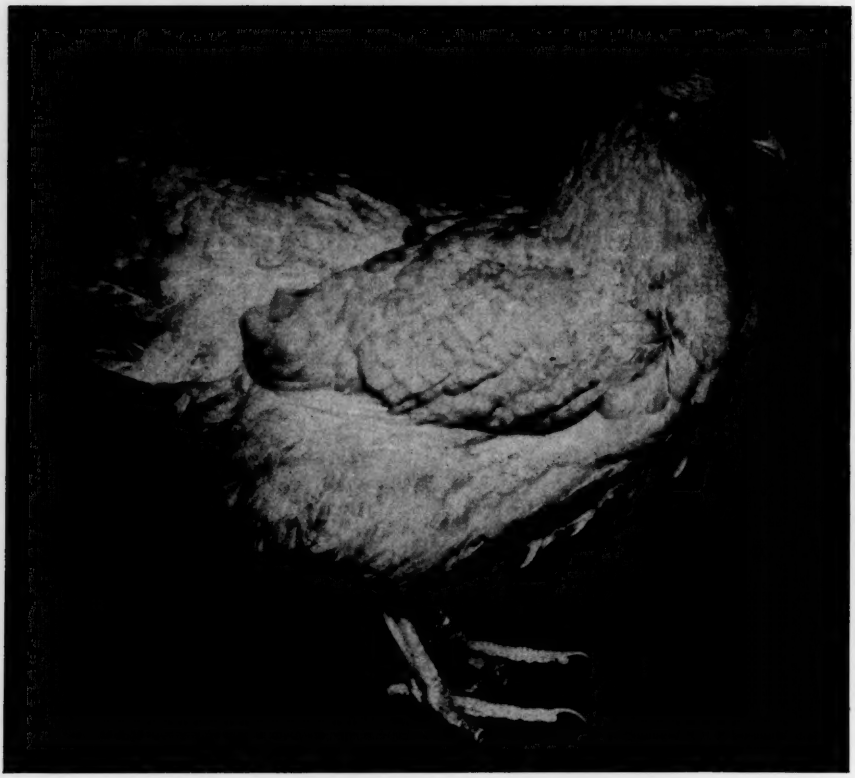
‡Albinism, in the restricted sense used here, means the loss of melanic pigment in skin, feathers, and eyes.



AN IMPERFECT "ALBINESS"

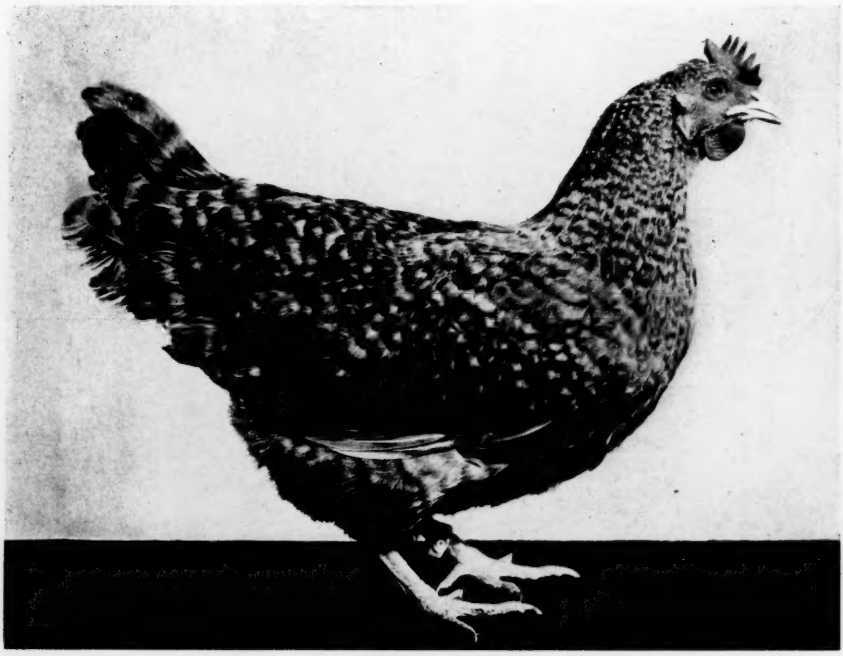
Figure 14

Barred Plymouth Rock female with sex-linked albinism, showning a faint "ghost barring."

is obscured by dense pigment in the retina and iris. As the chicks age, the irides become a blue-gray color, and gradually the eyes assume nearly normal appearance except for the dull red pupils. Excised eyes clearly show a deficiency of pigment, but it is apparent even macroscopically that the iris and ciliary body contain some melanin.

To get material for microscopic examination, eyes of day-old chicks were removed and placed in Bouin's fluid after slicing through the wall of the eye at the corneo-scleral junction to allow better penetration of the fixing agent. The eyes were left in Bouin's fluid from 1 to 15 days, after which they were dehydrated in ethyl alcohol, cleared in toluene, and embedded in paraffin. Sections were cut at a thickness of 10 microns, and stained with Ehrlich's haematoxylin, Mallory's triple stain, or Mayer's HCl-Carmine. Unstained sections proved to be particularly useful for comparisons of pigmentation in eyes of normal and albinotic chicks.

Microscopic examination reveals a small amount of melanic pigment in the albinotic eyes, but it is limited to the retinal pigment layer and the retinal portions of the ciliary body and iris. In these parts of the eye, the small number of scattered pigment granules causes a brown appearance, whereas the densely



A "PINK-EYED" HEN
Figure 15

A Barred Rock Hen, homozygous for the "pink-eye" gene. Pigmentation of the feathers is much reduced, but not so much as by the sex-linked gene *al* (Figure 14). From Warren.[11]

packed granules in eyes of non-albinos from the same matings make these same parts an intense black (Figure 19 *P.e.*). There is no pigment in the sclerotic or choroid layers or in the pecten, structures which are heavily pigmented in the normal eyes studied for comparison.

Albinotic embryos can be easily recognized at five days of incubation by the lack of melanin in their eyes.

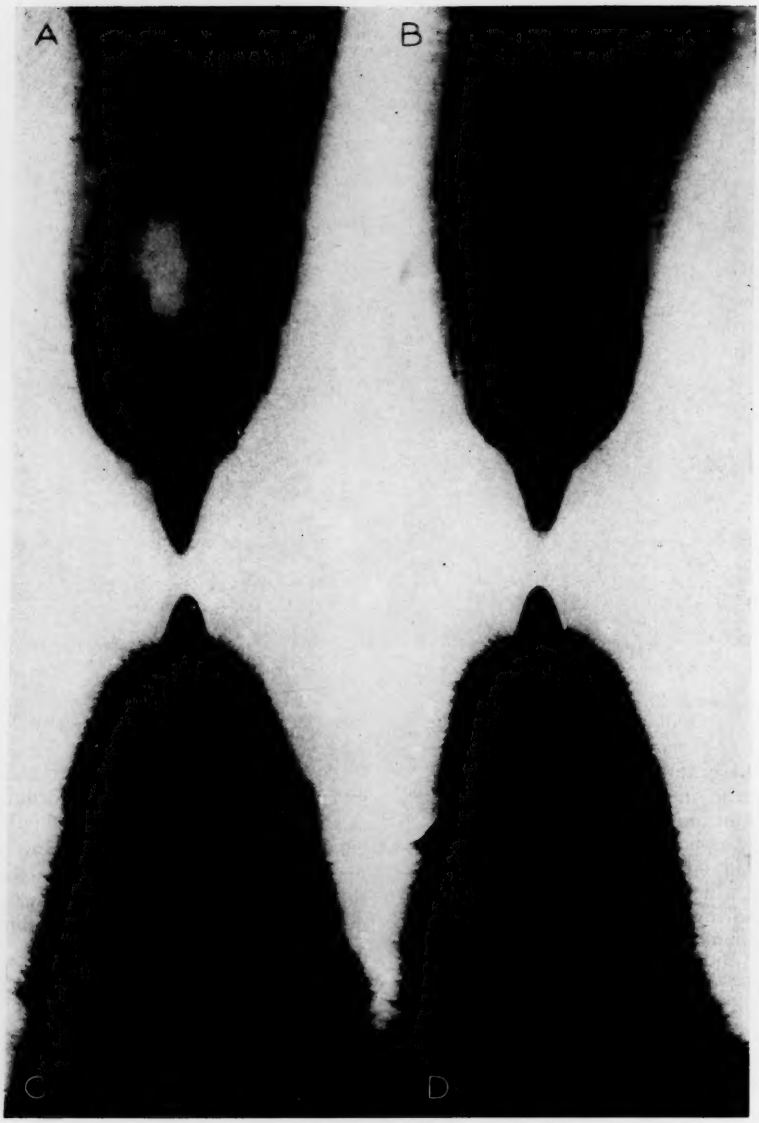
C. Classification

Pearson, Nettleship, and Usher[8] proposed the following useful classification of different degrees of albinism:

Total: complete absence of melanin.
Incomplete: eyes, skin, or hair (feathers) affected, but not all three.
Imperfect: partial inhibition of pigment-formation in any or all of these three seats of pigmentation, but not total absence of pigment in any.
Partial: complete or partial inhibition of pigment-formation within localized areas, as in piebald albinism.

From the description of our albinos given above, it is clear that according to this classification the mutation should be labelled as imperfect albinism. However, for convenience and brevity, the condition is hereafter mentioned in this paper merely as albinism and the affected birds as albinos.

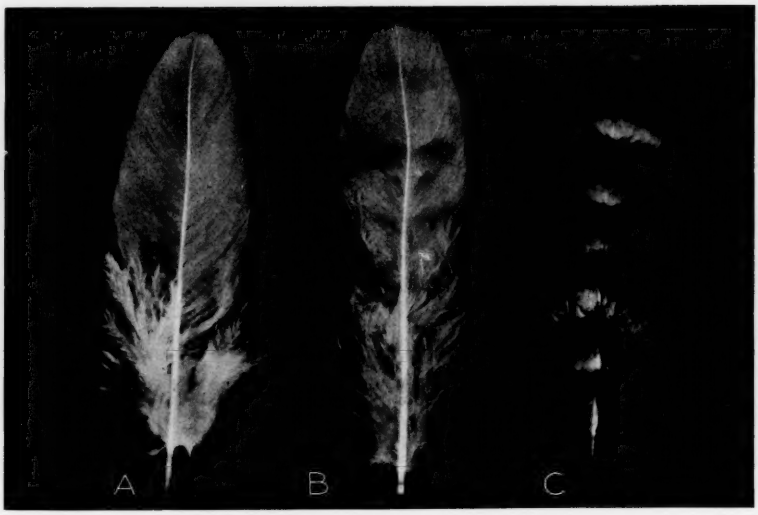
This new mutation inhibits the formation of melanin somewhat less than the autosomal albinism in the fowl described by Warren.[10] On the other hand, it reduces pigmentation much more than does the "pink-eye" mutation (Warren[11]), which, like ours, causes imperfect albinism. It happens that this difference can be nicely shown because Warren's pink-eye mutation was found in White Rocks, which are genotypically barred as are normal Barred Rocks. Dr. Warren has kindly made available the illustration used in his paper. We are thus able to



EFFECT OF *AL* GENE ON CHICK PATTERNS

Figure 16

(*A*) Barred and (*B*) non-barred albinotic chicks contrasted with (*C*) barred and (*D*) non-barred normal siblings. The unpigmented head spot in *A* and *C* shows that they carry the gene for barring. The albinos have shorter down.



BARRING ON WING FEATHERS

Figure 17

Feathers from wing-bow region of (*A*) a White Leghorn, (*B*) an albinotic Barred Rock, and (*C*) a normal Barred Rock. Dark bars are faintly visible in the feather from the albino.

show two barred females, one of which (Figure 14) has the pigment reduced by our sex-linked, imperfect albinism, the other (Figure 15) by Warren's autosomal pink-eye mutation. A striking contrast is evident in the plumage.

Genetics

The original albinotic Barred Rock pullet was mated in November, 1939, to a Single Comb Black Minorca male. An F_1 generation of 15 normally pigmented chicks proved that the albinism was recessive. As was to be expected, the male offspring were all barred, the females black and non-barred.

It seemed possible at that time that the condition might be the same as the recessive autosomal albinism described by Warren[10] or the pink-eye mutation which he has more recently reported.[11] To test these possibilities, Dr. Warren kindly supplied two males, one homozygous for his albinism, the other for pink-eye. Matings of the Cornell albino female in turn with these two Kansas males yielded the following results:

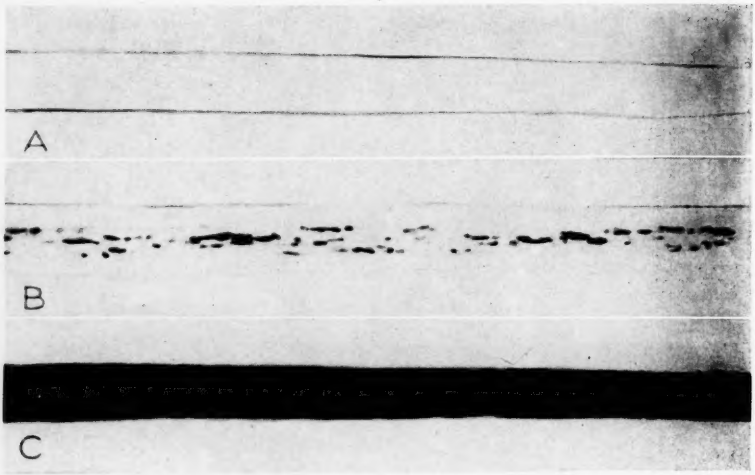
Parents	*Progeny*
Cornell ♀ × Kansas albinotic ♂	7, all colored
Cornell ♀ × Kansas pink-eye ♂	16, all colored

It was clear from this that the albinism being studied at Cornell was genetically distinct from the two other types of albinism thus far reported in the fowl.

F_1 males from the original albinotic female became mature in April, 1940, and were mated with (*a*) their sisters, (*b*) unrelated New Hampshire females, and (*c*) their dam. The results of these matings, given in Table 1, clearly prove that a single gene is responsible for the albinism and that it is sex-linked.

The mating of F_1 males to New Hampshire females is sufficient to prove this fact. These hens were quite unrelated to the F_1 males and the possibility that they carried the same gene for albinism was extremely remote. The facts that about half of the female progeny of this mating were albinos,* and that none of the male progeny was albinotic, can be explained only on the basis that the F_1 males carried albinism in one sex chromosome.

*Yclept by lexicographers *albinesses*!



PIGMENT IN CHICK DOWN

Figure 18

Photomicrographs showing portions of chick down from (*A*) a White Leghorn, (*B*) an albino, and (*C*) a Barred Plymouth Rock. All ×660. The contrasts show the extent to which the pigment is present, but reduced in amount, in the albino.

Since the F_1 females could not have carried the sex-linked gene, the F_2 generation (Table 1, mating *a*) should show the same ratio of normals to albinos as is found in progeny from the outcross to the unrelated New Hampshires. For a simple recessive sex-linked gene this ratio should be: 2 normal ♂ ♂ : 1 normal ♀ : 1 albinotic ♀. The data in Table 1 show for both of these matings a reasonably close fit of the numbers actually observed in each class to those expected on this basis. There is an excess of *albinesses* above expectation (which is discussed later), but not enough to raise any question about the genetic basis for the mutant character.

In the progeny from the back-cross (Table I, mating *c*), approximately equal numbers of normal and albinotic chicks were found in each sex, as was expected. This mating provided the first homozygous males. In appearance, viability, and sensitivity to light, these did not differ noticeably from the hemizygous albinotic females.

Since the symbol, *a*, has already been preempted by Warren for his autosomal albinism, it is proposed to designate this sex-linked gene by the symbol, *al*.

Other Effects of the Gene

Viability. In wild animals, albinism is generally considered to have an adverse effect upon viability, chiefly because the albinos are usually extremely sensitive to strong light and frequently have defective vision. Presumably, these handicaps, together with the conspicuousness of such animals, make them easy victims of predators. Of 18 albinotic mockingbirds studied by McIlhenny,[7] only two survived for as long as six months and these were kept in captivity.

Records show that during embryonic development, and in the first two weeks after hatching, the albinos described in this paper were fully as viable as were their normal siblings. Disregarding embryos that died up to five days of incubation (*i.e.* before albinism could be recognized), figures for the two classes are as follows:

	Albinos		Normal	
	Number	*%*	*Number*	*%*
Number observed	149	.....	357	.....
Dead embryos	32	21.5	83	23.2
Hatched chicks	117	78.5	274	76.8
Died to 2 weeks	21	17.9	56	20.4

Among 70 albinotic offspring from three different matings, mortality to six months of age was 20 per cent, which is not excessive for late-hatched chicks such as these were.

Reproduction. Albinism certainly did not impair the capacitv for reproduction of the original albinotic female. She laid 240 eggs in her first laying year of 365 days from the date of first egg, and 284 eggs in her first fifteen months of egg production. During most of this period she was kept in a cage by herself in a laying battery. This record is considerably better than the average for other unrelated Barred Rock pullets in the same year. The hen was mated with various males and, of 95 eggs incubated, all but one were fertile. From these, there hatched 84 chicks, or 89 per cent of the fertile eggs, which is unusually good. However, the effect of the gene on reproduction cannot be measured adequately by the record of this one outstanding female. Albinotic pullets hatched in 1940 are beginning to lay at a normal age.

Plumage. The down of albinotic chicks appears to be shorter than that of normal chicks. The contrast between the two is hardly as distinct as the difference between "rex" rabbits (in which the long guard hairs are shortened) and normal ones, but it is somewhat the same. This is evident in Figure 16. The albinos seem to feather out more slowly than non-albinotic siblings when both have the same genotype with respect to the sex-linked gene for rapid feathering.

Sight. Sight of the albinotic birds seems little impaired, but critical tests have not been made in different degrees of light.

Excess of Albinos

In the progeny from matings of males carrying albinism to sisters and unrelated females (Table I, matings *a* and *b*), there were more albinos than were expected. For convenience, the data for these two matings together are summarized in Table II.

Considering the whole population, there was an excess of 23 albinos, or 19 per cent, above the 118 expected. This is interesting, especially because in McIlhenny's[7] mockingbirds there was also a considerabe excess of albinos above the 25 per cent expected. Testing the significance of the deviation from expectation in our data by the χ^2 test yields a value for χ^2 of 6.01 and for P of .014. According to orthodox biometrical reasoning, this would mean that the excess of albinos is greater than could be expected by chance more often than once in about 70 trials, and is therefore significant.

However, there is also a rather high proportion of females in this same population. From the many studies of the sex-ratio in the fowl it seems that the normal secondary sex-ratio for this species is about 49 ♂♂ to 51 ♀♀. The expectations in Table 2 are based on these figures. The excess of females was 22, or 9 per cent, above the expected number of 236. Tests for significance of this deviation yield a value for χ^2 of 4.18 and for P of .043. The surplus of females was therefore almost statistically significant.

TABLE I. Matings proving imperfect albinism to be sex linked.

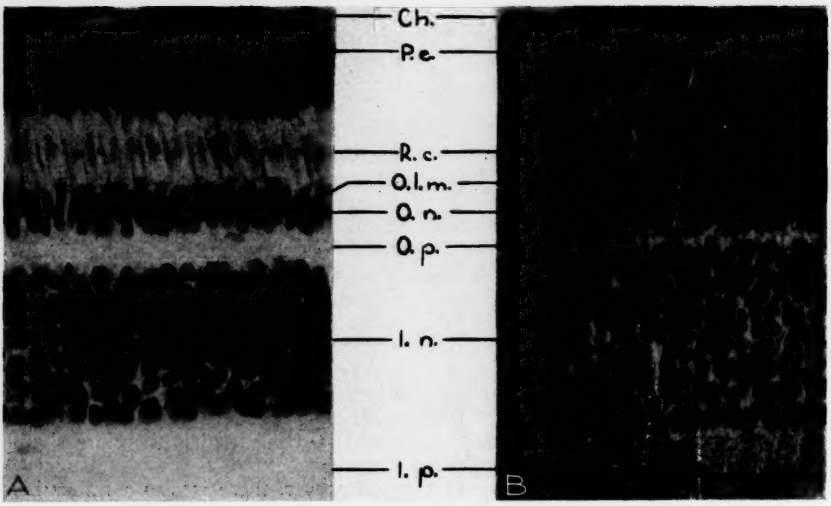
Matings of F1 ♂♂	*Progeny** Normal ♂♂	Normal ♀♀	Albinotic ♂♂	Albinotic ♀♀
(a) to F1 ♀♀	62	32	0	41
Expectation	67	34	0	34
(b) to New Hampshire ♀♀	143	85	0	100
Expectation	164	82	0	82
(c) to albinotic dam	7	6	8	5
Expectation	6.5	6.5	6.5	6.5

*About 87% of these were chicks that hatched, the remainder embryos that died during the last 3 days of incubation.

TABLE II. Sex ratios and albinos in progeny of F1 ♂♂ × normal ♀♀.

	Normal	*Albinos*	*Totals*	*Expected**
Males	205	0	205	227
Females	117	141	258	236
Total	322	141	463	.....
Expected*	345	118	.....	463

*With a sex ratio of 49 ♂♂ : 51 ♀♀.



EYE PIGMENTATION

Figure 19

Photomicrographs showing portions of retinae from eyes of a day-old albinotic chick (right) and its normally pigmented sibling (left). Pigmentation is quite intense in both the pigment epithelium and choroid of the normal, but in the albino occurs only in the pigment epithelium and there in small amounts MCl-Carmine, 10 μ. ×440.

Abbreviations: *Ch.*—choroid; *P.e.*—pigment epithelium of retina; *R.c.*—layer of rods and cones; *O.l.m.*—outer limiting membrane; *O.n.*—outer nuclear layer; *O.p.*—outer plexiform layer; *I.n.*—inner nuclear layer; *I.p.*—inner plexiform layer. The inmost portion of the inner plexiform layer and the ganglion cell layer are not shown.

Since all albinotic chicks from these matings were females, any surplus of females in this population would automatically tend to increase the proportion of albinos, assuming that spermatozoa bearing *Al* or *al* were equally effective in fertilizing ova destined to produce females. An apparent excess of albinos could thus be caused, not by any peculiarity associated with albinism, but rather by embryonic mortality affecting males more than females, by any peculiarities of gametogenesis causing the dams to yield more females than males, or, as seems more probable in the present case, by chance variations.

For this reason, the excess of albinos should be studied in the female population only. Here, where equal numbers of normals and albinos were expected, each heterozygous sire produced more albinos than normals:

	Progeny	
Male	*Normal*	*Albinos*
G5021	67	82
G5022	31	35
G5023	19	24
Totals	117	141
Expected	*129*	*129*

This consistency is interesting, but application of the χ^2 test to the totals for the combined data shows that the deviation from expectation is not significant, χ^2 being 2.23 and P .14.

In man, an excess of albinos over the 25 per cent expected is found in populations comprising sibships containing one or more albinos. It is well known, however, that this results from the inclusion in these populations of small families in which albinos occur, and the exclusion of small or large families from heterozygous parents whose genotypes are unrecognized because by chance all their children were normal. Cockayne's[1] tabu-

lation of the many sibships containing albinos studied by Pearson, Nettleship, and Usher, by the Davenports, and by Harris, shows clearly that the proportion of albinos is closer to expectation in sibships of six or more, and still closer in sibships of nine or more.

Comparative Genetics

The literature on ornithology contains many references to "albinos," most of which are not true pink-eyed albinos at all, but dark-eyed birds lacking more or less of the coloration normally found in the plumage. In the microscopic examination of the eyes of 28 birds with various degrees of albinism (many of which were dark-eyed) Usher[8] found only one, a greenfinch, *Chloris chloris,* that was entirely without melanin. Some of the others showed imperfect albinism resembling somewhat that described in this paper.

The number of cases of albinism in birds that have been studied genetically is small. The recessive autosomal albinism and the pink-eye mutation in the fowl, both investigated by Warren, are the only other cases in that species known to the writers. In the pink-eyed birds, the reduction of pigment in the plumage is slight and histological studies of the eye have not been reported.

McIlhenny[7] has recently described a type of true albinism in the mockingbird, *Mimus polyglottos,* which, from the proportion of albinos observed over five years in the progeny of heterozygous parents, was evidently a unifactorial recessive character. The fact that 15 offspring from the heterozygous male by a second mate were all normal proved further that the mutation was autosomal, a point overlooked in the original report.

The white robins (*Turdus migratorius*) illustrated by Cook,[3] together with the reports of other albinotic robins in the locality whence they came, suggest a case of hereditary albinism in that species, although it is not clear from the record that they were pink-eyed albinos. The present authors observed this year at Ithaca a pink-eyed, pure white robin whose three nest-mates were all fully pigmented. Unfortunately, only one brood from this mating was found. The albinotic bird died shortly after leaving the nest.

A sex-linked albinism studied in the budgerigar, *Melopsittacus undulatus,* by Kokemüller[6] apparently eliminates melanin and the structural blue color found in one mutant form of that species, thus making it a pink-eyed albino. These colors are also eliminated in the "wild type" green birds, but the lipochrome pigments are unaffected. The result is a bright yellow, pink-eyed budgerigar.

One of the first sex-linked genes known in birds was studied in cinnamon canaries by Durham and Marryat.[4] Affected birds had pink eyes at hatching but these darkened with age. Although these canaries were considered as having a chocolate pigment rather than a black melanin, it seems possible that the cinnamon plumage and pink eyes might have been caused by a gene for imperfect albinism acting upon some kind of melanoprotein.

Pearson, Nettleship, and Usher[8] include in their monograph four pedigrees showing sex-linked inheritance of albinism of a type apparently somewhat imperfect in man.

The effects of the *al* gene in the fowl are similar to those caused by the autosomal albinotic dilution in cattle reported by Cole *et al,*[2] in that retention of some of the melanin causes a "ghost pattern" to show in the body covering. In both cases histological examination showed elimination of pigment to be incomplete.

Discussion

This mutation adds one more to the 23 genes previously assigned to six linkage groups in the fowl (Hutt and Lamoreux[5]) and raises to 9 the number known to be located in the sex chromosome. Experiments are in progress to determine the linkage relationships of albinism to other sex-linked genes. These have been complicated somewhat by the fact that albinism prevents the expression of silver and gold, and makes difficult the definite identification of barring. The new mutation has the advantage that

albinotic chicks are always sharply distinct from others.

Only a single albinotic chick was found by Mr. Babcock in about 8,000 Barred Rocks from the flock that yielded the original albinotic female. This suggests that the mutation had recently occurred in the germ cells of the sire and that at most only a small proportion of his spermatozoa could have carried it. Mr. Babcock states that there were about 30 males in the parent flock from which the albino was hatched, and that all the parent birds were normally colored. Assuming random mating and equal hatchability of eggs, each male would sire about 270 chicks. If the mutation had occurred in the previous generation, it would have been present in half the germ cells of any male carrying it, and, by chance, such a sire should have yielded about 65 albinotic female progeny. While considerable deviations from this expectation could have been caused by preferential mating, differential fertility, and other variable conditions, it seems reasonably certain that if the mutation had occurred a generation earlier, more than one albinotic chick would have been found. This is particularly so because embryonic mortality falls no more heavily upon albinos than upon their normal siblings.

In one way a sex-linked mutation such as this affords a special advantage to the biologist. A carrier male will produce the mutation in about half his daughters when he is mated to normal, but quite unrelated, females. Embryological and physiological studies of the mutation may therefore be carried out without the undesirable inbreeding required to maintain stocks homozygous for any autosomal recessive character.

Summary

Imperfect albinism occurring in Barred Plymouth Rocks was found to be caused by a sex-linked recessive gene to which the symbol, *al,* is assigned. Inhibition of the formation of melanin is not total, since affected birds may show "ghost-barring" in the plumage. Histological examination revealed the presence of black pigment in the eye and plumage.

Sight of the albinotic birds seems little impaired, and the viability of albinotic embryos and chicks is as good as that of normal ones. Other cases of genetic albinism in birds are briefly discussed. There is evidence that the mutation was found in the first generation after its occurrence.

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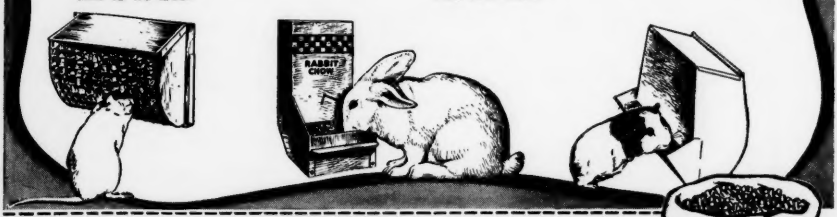

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